Dissertation

POPULATION DYNAMICS AND FACTORS AFFECTING SPINY LOBSTER SMALL SCALE FISHERIES

Soledad Luna

Technische Universität Dresden

Fakultät Umweltwissenschaften

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M.Sc. Soledad Luna

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Gutachter:

Prof. Dr. Uta Berger

Prof. Dr. Thomas Berendonk

Prof. Dr. Volker Grimm

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LIST OF ABBREVIATIONS

CL Carapace length/cephalothorax length
ETP Eastern Tropical Pacific
IBM Individual based model
IUCN International Union for the Conservation of Nature
MLS Minimum landing size
ODD Overview Design Details
PVA Population viability analysis
SOM Size of onset sexual maturity
SST Sea surface temperature
TL Total length
TNC The Nature Conservancy
WWF World Wildlife Fund
UNEP United Nations Environmental Programme

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ABSTRACT

This dissertation analyses the effects of current fisheries practices and management regulations of the green spiny lobster (*Panulirus gracilis*) in the Eastern Tropical Pacific Region (ETP). *P. gracilis* has reached a critical state in the ETP. Country-based studies report that between 60 and 98% of lobsters caught in the wild are under the minimum landing size (MLS). This means that spiny lobsters are being extracted before reproducing and contributing to the replenishment of interconnected populations. The recovery of green spiny lobster populations in the ETP and the future maintenance of a sustainable fishery will depend on effective management decisions and on taking in account environmental factors that influence the population dynamics of the lobsters.

In the first study (Chapter 2), the B52 Spiny Lobster individual based simulation model was used for conducting a population viability analysis to quantify the effect of current fishing practices and the effect of varying management regulations on minimum landing size (MLS) and fishing effort. The best suit of regulations to maintain the highest abundance, production of offspring and catch is to protect juveniles and egged females, and to establish a MLS that assures the reproduction of individuals before being extracted. This study revealed regional variations, however the patterns and the causes for variation were not yet clear. This led to the next chapters in this dissertation.

In Chapter 3, I used a meta-analysis to explore regional lobster variability by comparing published studies from the ETP. The objective was to identify patterns of variation related to geographic and environmental factors of the region that can inform the establishment and evaluation of coordinated regulations. Morphological relationships showed to be more variable at northern latitudes, where the mean annual sea surface temperatures are higher than at lower temperatures at the Equator. In terms of management, MLS regulations should be adapted accounting for the effect of sea surface temperature and its variation. Additionally, it was observed that monitoring methodologies are not standardized within the region and even in some cases, neither within countries. Furthermore, in most places monitoring of the spiny lobster fishery happens sporadically, only in Galapagos takes place every year. Identifying patterns of variations can improve the accuracy of prediction models which can help to explore, design, and apply more effective management measures, as well as promote regional coordination to support the recovery and maintenance of spiny lobsters.

In Chapter 4, I contrast current Ecuadorian minimum landing size (MLS) regulation to lobster empirical measurements within Ecuador in order to recognize potential pitfalls for management enforcement. I used linear regression and multiple regression models with the objective of identifying potential relative size variations of the individuals caught in the wild over time and in the different fishing areas in Ecuador, as well as to analyse the effect of locality, sex, age and mean SST on the tail length/total length ratio. Morphological relations were significantly different among sexes, in time and by all sites. Most importantly, this study shows that current minimum size regulations are not applicable to all sites. Additionally, I found that water temperature has a significant effect on morphological relationship variations. However, it was not the main site-specific variable responsible for explaining such variations. In general, this work emphasizes the need for length data collection standardization and the consideration of temporal and spatial variation implications in national and regional fishery management planning, enforcement and evaluation.

Key words: *Panulirs gracilis*, *Panulirus penicillatus*, individual based model, population viability analysis, small scale fishery, meta-regression, random effects model, fixed effects model, multiple regression.

CHAPTER 1

1 GENERAL INTRODUCTION

Spiny lobsters, as well as other lobster species, were so abundant and accessible during the 1800s and early 1900s that were regarded as food for the poor. As a matter of fact, excess lobsters were used as soil fertilizer. Lobstering was done by gathering them by hand along the coast in intertidal areas (Maine State Archives collection, com. pers. artisanal fishermen in Ecuador). Workers at that time demanded to include in their contracts that they won't accept to eat lobster more than once per week. Nowadays, lobsters are a commodity with prices ranging among the most expensive common marine products (Lipcius & Eggleston, 2000) and the public demand for this good keeps increasing. In fact, in 2014, lobster catches worldwide marked a new record (FAO, 2016). The clawed American lobster (*Homarus americanus*) and the Norway lobster (*Nephrops norvegicus*) account for 60% of the global lobster fishery, followed by the Caribbean spiny lobster (*Panulirus argus*) and various *Panulirus* spp. in Africa, Asia, the Americas, and Oceania (FAO, 2017). The International Union for Conservation of Nature and Natural Resources-IUCN (2017) evaluated the American and Norway lobster populations' trend as stable. However, population status of other extracted lobster species varies around the world. Fisheries studies worldwide have reported a decline in the catches (Sundelöf et al., 2015; Raúl Pérez-González, 2011; Pollock, 1993; Breen, 1994; Puga et al., 2010), and a reduction of the mean size of the caught individuals (Guzmán et al., 2008; Campos, 1993; Loesch & Lopez, 1966; Villón et al., 2000).

In this study, the focus is on the green spiny lobster (*Panulirus gracilis*) in the Eastern Tropical Pacific (ETP) region. The green spiny lobster *P. gracilis* is among the *Panulirus* species that contribute to the important fisheries in their region of distribution and main source of income for many small scale fishermen (FAO, 2017). Common management regulations in the region include an egged female moratorium and a minimum landing size (MLS) estimated and enforced by each countries' fisheries management authorities. Country-based studies report between 60 and 98% of lobsters under the MLS in the catch (Figueroa & Mero, 2013; Guzmán et al., 2008; Loesch & Lopez, 1966; Murillo et al., 2013; Naranjo Madrigal, 2011; Villón et al., 2000), except for Galapagos where reported undersized individuals reach between 5 to 10% of the total catch (Espinoza et al., 2001; Hearn et al., 2004; Ramírez, Reyes, & Schuhbauer, 2013).

Minimum landing size (MLS) is the most applied regulation for lobster fisheries worldwide. They assure that individuals reproduce before being exploited. MLS has been established and evaluated using estimates of the size of onset maturity (SOM) and yield-per-recruit assessments. In this study, SOM was used. SOM is the size at which a proportion of 50% of the females in a population have attained sexual maturity. Most commonly, lobster MLS is expressed as the length of one or more body parts. For example in Mexico, Panama and Costa Rica, MLS is expressed as the carapace length, whereas in Ecuador MLS is given in two measurements - the total length and the tail length (see Figure 5.1 in Chapter 5 for lobster body parts). For ease, fisheries record only the body parts used to express

the MLS as defined locally. For instance, the carapace, the tail, or the total length might be used. Very rarely are two or more body parts measured. The body parts that were not measured are calculated using length-length linear relation equations. Such equations are accepted and used as standard models to calculate the missing size based on the existing data, assuming relative sizes maintain a constant ratio. In this way, morphological relationships (such as the length-length linear relation) use the empirical field data to produce the standard statistics for stock assessment, management and fishery regulations.

Previous studies show that lobsters are able to react quickly to changes in temperature and food availability. Temporal and spatial varying conditions may affect lobster population dynamics, growth rates and relative growth, influencing also fisheries performance. In the same way, SOM for the same species may vary at geographical scales, due to changing environmental conditions such as temperature, due to density-dependence and due to fishing pressure (Green et al., 2014; Naranjo Madrigal, 2012; Quinn & Rochette, 2015; Serfling & Ford, 1975). Such variations are important to consider in order to design appropriated management regulations, inclusively MLS. Furthermore, these regulations have to be periodically revised and adapted, as well as their enforcement strategies. Additionally, the awareness and accountability of these variations should contribute to regional management planning to enhance local lobster populations.

Spiny lobsters, as other lobsters, have a life cycle characterized by a long pelagic larval stage (*Phyllosoma*) of around nine months. After traveling for thousands of kilometers with the major superficial and underwater currents, young spiny lobsters (*Puerulus*), settle in small crevices at shallow coasts. This pelagic larval stage allows broad dispersal and interconnection to other populations in the ETP (Pollock, 1993). Therefore, local recruitment is detached from local reproduction and the persistence of spiny lobster populations at one locality does not only depend on the local management efforts (Caley et al., 1996). However, in the ETP there is no regional oversight of the spiny lobster populations' state, their variability, possible variability causes and their influence on management planning, as well as enforcement. No collaboration is in effect to identify key source populations nor focus areas for conservation.

In this study, I explore the effect of the current and potential management regulations, the patterns of regional and country level variations, and the possible environmental and geographic causes of variation. For this, I employed an individual based population viability analysis, a meta-analysis, and single and multiple regression analysis. The aim is to evaluate the effect of measures and identify further considerations to adapt regulations.

This document covers five chapters. In this first chapter, I present the research objectives, introduce the methods used to address the research questions, and present the species and the study site. Chapters 2 to 4 focus on each of the research objectives and Chapter 5 offers an overall concluding discussion.

1.1 Research objectives

The general objective of this dissertation is to contribute to fisheries management by understanding the effect of current and potential regulations on the population dynamics of a species of spiny lobster. Furthermore, I explored regional and national morphological variation patterns and potential causative factors. The case study used for this thesis is the artisanal fishery of green spiny lobster (*Panulirus gracilis*) which takes place in all countries along the coast of the Eastern Tropical Pacific (ETP), from Baja California to northern Peru and the adjacent continental and oceanic islands.

Documentation on this fishery shows clear signs of decline such as a reduction in abundance and mean sizes of capture. Furthermore, fisheries monitoring report high percentages of juveniles in the catches. Managers and authorities are pondering to adapt management regulations especially regarding size limits and the prohibition of extracting egged females. An individual based population viability analysis, a meta-analysis and multiple regression analysis were used to infer the behavior of populations under different management regimes and reveal regional patterns (Figure 1.1). This study will therefore, address the following overall research question:

> How do current fisheries management regulations and regional factors influence the population dynamics and fisheries management of *P. gracilis*?

In the first study (Chapter 2), the B52 Spiny Lobster individual based simulation model was used for conducting a population viability analysis. The B52 model was implemented in Vortex 10, which is a free software developed by the Chicago Zoological Society and supported by the IUCN. The model was parameterized using empirical and values from the literature to simulate the dynamics of a virtual green spiny lobster population. The case example used is the green spiny lobster *P. gracilis* in the ETP. The objective of this chapter is to quantify the effect of current fishing practices on the population size, the production of offspring and the catch, as well as to explore the effect of varying management regulations on minimum landing size (MLS) and fishing effort. The research question is:

> What is the effect of the current fishing practices on the spiny lobster population?
>
> How would potential management adaptations in the MLS regulation and fishing effort affect the population size, the production of offspring, and the catch?

Spiny lobsters' population dynamics are characterized by an open cycle. This means that the persistence of spiny lobster populations at one locality does not exclusively depend on the local management efforts. Local recruitment is detached from local reproduction by a scattering larval phase. The prevalence of the reproductive population in oceanographically inter-connected localities is key for the perseverance of the spiny lobster populations. Therefore, an appropriate and effective fisheries management, has to consider a regional exchange and collaboration. To the best of my understanding, there is no systematized regional knowledge or exchange of fisheries monitoring information and therefore, no regional awareness of the state of the inter-connected populations. In Chapter 3, I used a meta-analysis to explore regional lobster variability by comparing published studies from the ETP. The objective is to identify patterns of variation related to geographic and environmental factors of the region that can inform the establishment and evaluation of coordinated regulations. The research questions are:

> Does the green spiny lobster present regional patterns that can influence their population dynamics and thus, its management?
>
> Can these patterns be explained by latitude, sea surface temperature, and Chlorophyll a concentration?

Even though a regional scope seems to be most appropriated for planning management of the spiny lobster in the ETPS, regulations have been traditionally enforced and controlled by each nation's government. With or without some sort of coordination among countries in the region, governments and management authorities are obliged to keep managing this fishery. With the existing information they have to adapt or maintain their regulations. In Ecuador, the spiny lobster fishery has been regulated since the 50s. In the 80s, the legal minimum landing size was enlarged from 25 to 26cm total body length, to protect the population, since mean landing sizes were decreasing, and more egged females were being caught. Reports since the 60s until now, suggest that the population keeps

degrading in the mainland whereas in Galapagos seems to be stable. In Chapter 4, I contrast current Ecuadorian minimum landing size (MLS) regulation to lobster empirical measurements within Ecuador in order to recognize potential pitfalls for management enforcement. I used linear regression and multiple regression models with the objective of identifying potential relative size variations of the individuals caught in the wild over time and in the different fishing areas in Ecuador, as well as to analyse the effect of locality, sex, age and mean SST on the tail length/total length ratio. The specific questions are:

Is the current MLS regulation applicable to all areas in mainland Ecuador and Galapagos?

What are the additional factors that should be considered to calculate the MLS?

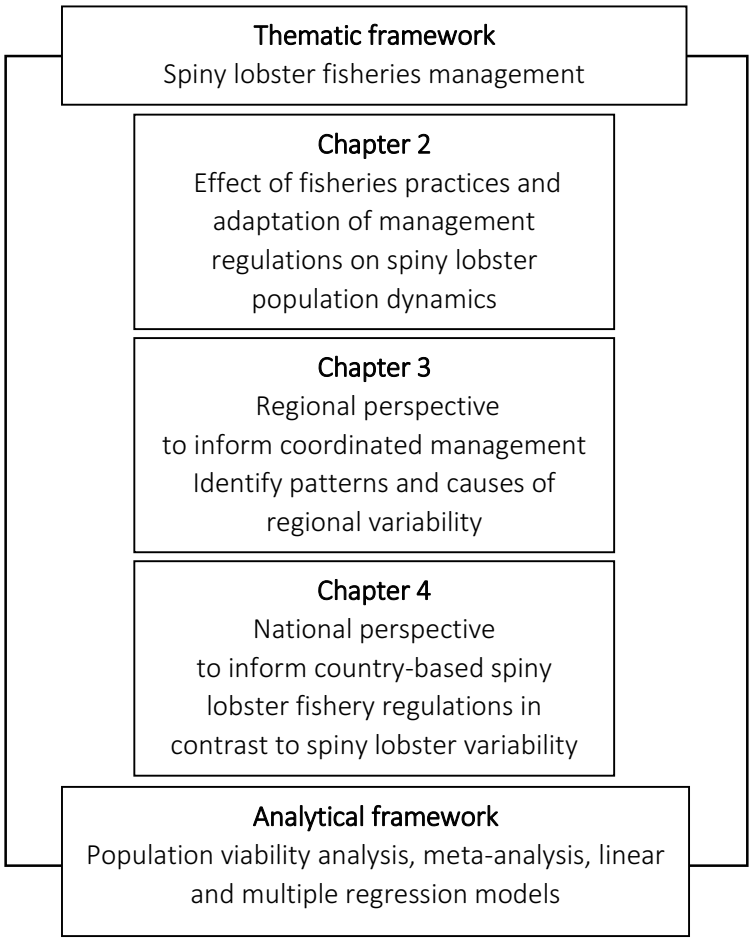

Figure 1.1 Thesis structure.

1.2. Panulirus gracilis

The green spiny lobster was selected for this study because it is the most widely distributed in the Eastern Tropical Pacific. Three more spiny lobster species inhabit parts of this region. Two of them

(*Panulirus interruptus* and *P. inflatus*) are mainly in the west coast of Mexico and California in the USA, and the third one (*P. penicillatus*) is almost exclusively in the islands of the ETP.

P. gracilis inhabits the eastern Pacific, from Baja California, Mexico to northern Peru, and the Galapagos islands. It occupies coasts with water depths between 0 to 40m, among rocks, in cracks and crevices (Briones-Fourzán & Lozano-Alvarez, 1992; Holthuis, 1991; Holthuis & Loesch, 1967). It is also found over sandy areas with gravel since it tolerates a wide range of water turbidity (Briones et al., 1981; Lozano et al., 1982; Pérez-González et al., 1992).

P. gracilis larvae go through a metamorphosis of eleven larval stages before settling in small crevices at shallow coasts. Larvae are able to travel for thousands of kilometers depending on the major superficial and underwater currents. As an example of their widespread movement, Cobb & Wang (1985) found *P. gracilis* larvae 4000 km away from any possible source. Johnson (1971) found high concentrations of *P. gracilis* between Galapagos, Mainland Ecuador, and Costa Rica, and around 2500 km to the West of Galapagos. This indicates that the persistence of spiny lobster populations at one locality does not exclusively depend on the local reproduction. Thus, populations in the region may be interconnected. However, the relative importance of each of the breeding populations is unknown.

The number of broods per year and the size of the brood are age-specific in spiny lobsters, as in other crustaceans (Chubb, 2000). *P. gracilis* can reproduce several times per year. Smaller individuals reproduce two times and larger can have at least four broods per year (Briones-Fourzan, 2014). Female lobsters carry eggs for three to four weeks while the embryo develops before hatching (Briones-Fourzán and Lozano-Álvarez 1992, Torres-Zepeda et al. 2008). Briones-Fourzan (2014) calculated that *P. gracilis* can carry a mean number of 1047 ± 87 eggs per gram of total body weight. Mero-Del Valle et al. (2015) determined for *P. gracilis* that females larger than 90 mm CL can be considered as mega-producers since their reproductive potential (total egg production / number of females per size class in relation to the total number of females) is the double in comparison to smaller females. In their study, Mero-Del Valle et al. (2015) determined that females smaller than 80mm CL generated 17.8%, females in the range of 80-90 mm CL generated 31.71%, and larger than 90 mm CL produced 38.2% of the total production of eggs. Size and weight-specific fecundity relations may have geographical and seasonal variations (Chubb, 2000).

The green spiny lobster in the ETP is subject to artisanal fisheries only. They are captured with hooka, SCUBA and free diving in places where waters are not turbid, and with nets in places with no or poor visibility like for example near river mouths (Bautil et al., 2003; Guzmán et al., 2008; Murillo Posada et al., 2013).

1.3 Methodology used

The analytical framework of this study is composed of three main methods (Figure 1.1): an individual based population viability analysis, a meta-analysis and a single and multiple regression analysis. The text below presents the methods used in further detail.

1.3.1 Individual-based Population Viability Analysis

Population viability analysis (PVA) are risk assessment analysis commonly used to assess the conservation status of small populations. PVA are used to quantify the probability of extinction, quasi-extinction or the probability of explosion of a population under the influence of external events and processes intrinsic to the population. PVAs are able to analyse and compare management scenarios

and thus, to produce traffic lists for supporting decision making (Burgman et al., 1993; Lacy et al., 2017; Lacy, 1993; Radchuk et al., 2013).

Simulation models, and particularly individual based models (IBM), are nowadays well accepted and used for PVAs (see for example Grimm & Storch, 2000; Hosack et al., 2002; Muhammad Ali et al., 2011; Penn et al., 2000; Pergams et al., 2000; Wiegand et al., 1998; Elderd & Nott, 2008). Individual based models (IBM) allow to account for the variability of the individuals' attributes and behaviors, to simulate populations or systems of populations (Berger et al., 2008; DeAngelis & Grimm, 2014; DeAngelis & Mooij, 2005). Previous lobster IBMs have explored juvenile behavior and reproducing aggregations of spiny lobster (*Panulirus argus*, Butler 2003), recruitment of spiny lobster in degraded nursery habitats (*Panulirus argus*, Butler at al., 2005), larval dispersal of American lobster coupled with biophysical dynamics (*Homarus americanus*, Incze et al., 2010), climate effects on mortality-based biological reference points for Pronghorn spiny lobster (*Panulirus penicillatus*, Chang et al., 2011), and the effect of alternative harvesting practices on the European lobster (*Homarus gammarus*, Sundelöf et al., 2015).

The B52 Spiny Lobster individual based simulation model used in this study, was implemented in Vortex 10 (R.C. Lacy & Pollak, 2014). Vortex 10 is a free computer program specially designed for conducting population viability analysis. Vortex 10 was developed by the Chicago Zoological Society and is supported by the IUCN Species Survival Commission's Conservation Breeding Specialist Group. It was designed to simulate a population by progressing through the sequential events that characterize the life cycle events of a species (such as birth, death, mating, and environmental disturbances). These events occur in accordance with probabilities modeled as constants or as random variables that follow specified distributions (Lacy, 1993, 2000). In this study, I parameterized the B52 model using empirical and published information to investigate the effect of the current and potential management regulations impact on the population size, offspring production, and catch of an exploited population of the green spiny lobster *P. gracilis*.

The ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006, 2010) is used to describe the B52 model (see Section 2.2.4 The B52 Spiny Lobster model in Chapter 2).

1.3.2 Meta-analysis

Meta-analysis allows to analyse statistically the results of individual scientific studies with the purpose of integrating the findings in one single analysis (Glass, 1976). Meta-analysis express the outcomes of the different studies in a common scale. The measure of outcome is called an "effect size" and expresses the magnitude of the result of interest (Koricheva et al., 2013). Effect sizes that represent the same research question across studies can be combined to produce a pooled mean effect size. However, a meta-analysis acknowledges that some studies are more precise or carry more information than others and therefore, should have a larger weight in the combined effect. In a meta-analysis, two models are used to assign weights based on different assumptions. The first, the fixed-effects model assumes that all studies share only one true effect size. This means that the influencing factors are the same in all study populations and variation is due to random error intrinsic to each study. Therefore, large studies will have a strong weight and small studies will be almost ignored. The second model, the random-effects, allows for variation of the true effect among studies, meaning that it accounts for the possibility that the differences among study populations could impact on the outcome. Variations are assumed to be due to random error within studies and due to true variation of the effect size among studies. Hence, in this case when assigning weights, small studies won't be discounted and large studies won't overly influence the combined effect (Borenstein et al., 2007).

Meta-analysis were first developed and used in medicine and social sciences (see for example Chalmers et al., 1977; Delmas et al., 2013; Rosenthal & Rubin, 1978) mainly to generalize the results of

individual studies reporting the pros and cons of treatments, to increase statistical power and detect small effects, and test the accuracy of diagnostics. In ecology and evolutionary biology, meta-analysis have been used since the 90s most commonly to identify large scale trends, and to investigate the causes of heterogeneity among studies performed in different habitats, environmental conditions or across geographical ranges (see for example Munguía-Rosas et al., 2011; Saldaña-Vázquez & Munguía-Rosas, 2013; Worm & Myers, 2003; Igulu et al., 2014; Harvey et al., 2013; Hedges et al., 1999). Previous lobster meta-analysis have investigated the geographic and environmental drivers of fecundity of the European lobster (*H. gammarus*, Ellis et al., 2015), the relative importance of top-down forces, such as fishing and predation, and bottom-up forces such as temperature, in regulating populations of the American lobster (*H. americanus*, Boudreau et al., 2015), and the effect of marine reserves on the abundance and size of the rock lobster *Jasus edwardsii* (Pande et al., 2008).

In this study, a meta-analysis was used to compare various regional studies and explore the variability in size ratios of the spiny lobster expressed as morphological linear relationship equations. I investigate the effect of sea surface temperature, Chlorophyll a concentration, absolute latitude and longitude as possible causes of heterogeneity across the Eastern Tropical Pacific. This variability should be accounted for when planning fisheries management at a regional scale.

A detailed description of the method is presented in Chapter 3, Section 3.2.

1.3.3 Single and multiple linear regression models

Single and multiple linear regression models enable to examine the relationship between one (single) or several (multiple) independent or predictor variables and one dependent variable. In this study, the variations of the spiny lobster length-length relations among sexes and sites were examined. A single linear regression analysis between tail length (dependent variable) and total length (explanatory variable) was performed to analyse changes in capture size over time and space. This analysis was completed by a multiple comparison of the slopes of another suite of linear regression models explaining the tail length with total length and locality as categorical variable. The multiple comparison of the slopes informed about the statistical significance of differences between the length-length ratios of all available studies. A multiple regression model was performed in order to analyze the effect of locality, sex, age and mean sea surface temperature (SST) on the tail length/total length.

1.4 Study site

This study targets the green spiny lobster *P. gracilis*, distributed only in the shallow coastal waters in the Eastern Tropical Pacific (ETP). The coastal and shelf areas of the ETP are classified as one of the twelve worldwide marine realms according to the Marine Ecoregions of the World (MEOW) classification system (Spalding et al., 2007). The surface pelagic waters of the ETP are one of the 37 Pelagic Provinces of the World (PPOW). MEOW and PPOW were elaborated cross-referencing various existing marine biogeographic classifications and aim to reflect patterns of biodiversity across habitats and taxa. It is the product of a collaboration among The Nature Conservancy (TNC), the World Wildlife Fund (WWF), the Ramsar Convention, the IUCN and the United Nations Environment Programme (UNEP). MEOW and PPOW are well accepted and used for assessing, priority setting, and planning marine conservation measures.

Realms and provinces, after the definitions of Spalding et al. (2007) and Spalding et al. (2012), refer to very large regions of coastal, benthic, or pelagic ocean across which biotas share a common evolutionary history. Realms and provinces have high levels of endemism driven typically by historical and broad scale isolation, water temperature, and the proximity of the benthos. As well as ocean

gyres, equatorial upwellings, upwelling zones at basin edges and semi-enclosed pelagic basins. The ETP is characterized by the encounter of several of the major current systems which results in a combination of tropical and temperate marine life. The presence of isolated islands, the confluence of currents and nutrient rich upwelling result in great diversity, endemism and aggregation of fisheries and tourism relevant species (Spalding et al., 2012).

The ETP is shared, from North to South, by southern USA, Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador and northern Peru. Each country has their own national level laws and institutions related to management of the marine resources and environments. Multinational agreements that are in place focus on prevention on marine pollution, and integrated coastal and marine ecosystem management (Heileman, 2009). Among the regional initiatives is the Eastern Tropical Pacific Marine Corridor, known for its name in Spanish CMAR (Corredor Marino del Pacifico Este Tropical, cmarpacifico.org). CMAR was established in 2004 with the aim of implementing regional governmental strategies to manage biodiversity and marine resources in order to assure a sustainable use. CMAR is comprised by a net of coastal and insular marine protected areas of Costa Rica, Panama, Colombia and Ecuador, with Galapagos, Coco, Malpelo, Gorgona and Coiba islands as core management areas (Figure 1.2).

International conventions and marine initiatives that govern in this region include the United Nations Convention on the Law of the Sea (UNCLOS), the Convention on Biological Diversity (CBD), the United Nations Fish Stocks Agreement, and the FAO Code of Conduct for Responsible Fisheries. Fisheries management efforts in the region are focused on migratory species and their most important by-catch species such sharks, and marine turtles, sea birds, and dolphins.

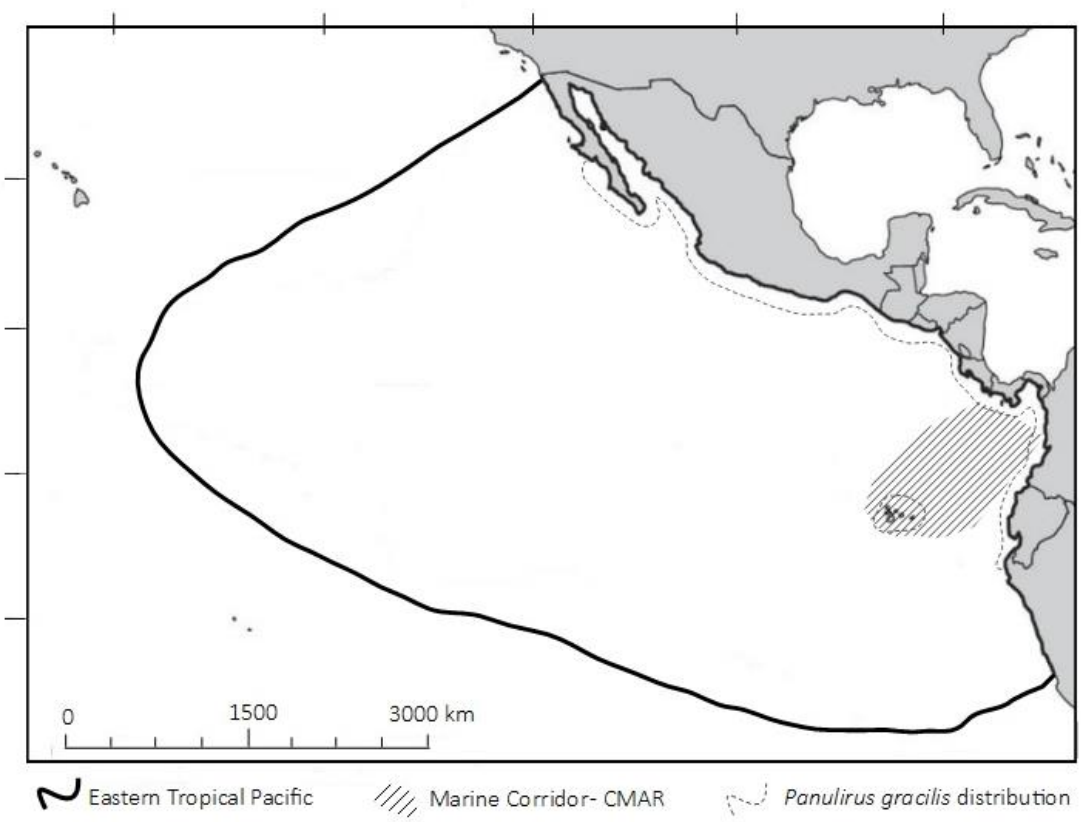

Figure 1.2. Map of the study area showing the Eastern Topical Pacific (ETP), the Eastern Tropical Marine Corridor (CMAR) and the geographical distribution of the green spiny lobster P. gracilis.

1.5 Data

1.5.1 Empirical data

Length-frequency data were collected between November 2009 and December 2011 from 2116 individuals of *P. gracilis* at the northern coast of mainland Ecuador, in Cape San Francisco, at the Galera-San Francisco Marine Reserve. The first year data proceed from fisheries landings collected with the compliance and help of the local artisanal fishermen. In the second year, a conservation agreement was established, which enabled the fishermen to create a non-take zone and monitor periodically the lobster population. Lobsters were caught by traditional fishing, using gillnets of 10.16 cm mesh size (stretched length), 1.5 m width, and 170 m length. Nets were extended over mixed muddy-rock floor substrata at a depth between 3 and 10 m and left overnight for 10 to 12 hours. Captured lobsters were generally alive, these were measured and then released back to the sea. For each individual captured, the carapace length (CL) and total body length (TL) were recorded (for lobster body parts see Figure 5.1 in Chapter 5). Throughout this study, these data are referred as "Luna, this study".

Additionally, a set of mark-recapture data from the Galapagos Marine Reserve was used. This program was run by the Charles Darwin Foundation and the Galapagos National Park Authority between 2001 and 2007. 57 females and 56 males of *P. gracilis* were caught by means of SCUBA diving and individuals were marked with a numbered T-floy tag and released. The number of *P. gracilis* recaptured was too low to make a reliable estimation of growth and therefore the resulting publication by Hearn & Murillo (2008) did not include the green spiny lobster. However, in this study these data are useful to calculate size conversion factors in Chapter 4. Throughout this study, these data are referred as "Hearn, not published".

1.5.2 Data from the literature

A review of literature was carried out using *Panulirus gracilis* and *Panulirus penicillatus* as key words in the following on-line databases: http.//www.scholar.google.com, http://www.jstor.org, http://booksandjournals.brillonline.com, http://www.sciencedirect.com (elsevier), www.scielo.org, http://www.springer.com, http://onlinelibrary.wiley.com, http://www.bioone.org. The search was not limited by year or journal. Peer-reviewed studies, as well as publications in local scientific journals, thesis manuscripts, NGO reports and governmental fisheries reports, were considered. Only those studies that took place along the Pacific coast between Baja California and northern Peru were chosen.

In Ecuador, I had access to physical grey literature. Therefore, institutional reports from the National Fisheries Institute (INP in Spanish), the Galapagos National Park Authority and the Charles Darwin Foundation were included.

The selected studies presented age at size, size at weight, length-length relationships, size at maturity (SOM), the methodology for measuring the different body parts, natural mortality and offspring size, the number of individuals assessed, their size ranges as well as management regulations such as MLS values.

1.5.3 Environmental data

Sea surface temperature (SST) and Chlorophyll a concentration data were used as environmental factors to explore their potential effect on spiny lobster regional patterns. Chlorophyll a concentration was considered as a proxy for photosynthetic biomass production, since there were no comparable benthos data at each site. Data were extracted for each location, for every month and every year while each selected study was carried out, and one year previous. SST data were extracted from the

AquaModis satellite online data base and Chlorophyll a concentration data were obtained from the SeaWifs satellite online database, in both cases using the free software SeaDAS (Baith et al., 2001).

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CHAPTER 2

Assessment of management strategies for the spiny lobster fishery in the Eastern Tropical Pacific: to fish and how to fish

ABSTRACT

Commonly worldwide management regulations for spiny lobster fisheries are the prohibition of extracting egged females and establishing a minimum landing size (MLS). These regulations aim to allow for reproduction and growth in order to obtain the highest yield possible over time. However, around the globe spiny lobster fisheries are severely reduced. This is the case of the green spiny lobster (*Panulirus gracilis*) in the Eastern Tropical Pacific (ETP), where countries document between 60% and over 90% of undersized individuals in their wild fisheries. The perseverance of spiny lobster populations in the ETP depends in part on the production of eggs of other interconnected populations. However, in the ETP there is no regional oversight of the spiny lobster populations' state and no collaboration is yet in effect to identify key source populations nor focus areas for conservation.
This study explores the effect of current management measures by means of the B52 Spiny Lobster model. The B52 model is an individual based population viability analysis model implemented in Vortex 10 and parameterized for the green spiny lobster to explore how the current fishing practices and management strategies influence the population size, the production of offspring and the catch. The B52 model shows that the best suit of regulations to maintain the highest abundance, production of offspring and catch is to protect juveniles and egged females, and to establish a MLS that assures the reproduction of individuals before being extracted. This is true if the MLS is calculated and implemented at an age or size larger than the SOM, for allowing individuals to reproduce one to three times before being extracted. An incorrect estimation of MLS, i.e. smaller than SOM or much larger than SOM, could lead the population to collapse or to under exploitation.

2.1 INTRODUCTION

Lobsters around the world were so abundant and accessible that they were regarded as the food of the poor during the 1800's and the mid 1900's in some less populated places. Indeed, lobstering was done by gathering them by hand along the coast (Maine State Archives collection, com. pers. artisanal fishermen in Ecuador). Nowadays they are a commodity with prices ranging among the most expensive common marine products (Lipcius & Eggleston, 2000) and the public demand for this good keeps increasing. In 2014, lobster wild catches worldwide marked a new record (FAO, 2016). The clawed American lobster (*Homarus americanus*) and the Norway lobster (*Nephrops norvegicus*) account 60% of the fishery, followed by the Caribbean spiny lobster (*Panulirus argus*) and various

Panulirus spp. in Africa, Asia, the Americas, and Oceania (FAO, 2017). At the same time, fisheries studies worldwide have reported a decline in the catches (Sundelöf et al., 2015; Raúl Pérez-González, 2011; Pollock, 1993; Breen, 1994; Puga et al., 2010), and a reduction of the mean size of the caught individuals (Guzmán et al., 2008; Campos, 1993; Loesch & Lopez, 1966; Villón et al., 2000). This is also true for the green spiny lobster *Panulirus gracilis* in the Eastern Tropical Pacific region (ETP). In the ETP, with the exception of Galapagos, fisheries data report that between 60 and 98% of the catch are individuals that have not reached yet the legal exploitable size (Murillo et al., 2013; Guzmán et al., 2008; Naranjo Madrigal, 2011; Pérez-González et al., 1992). Thus, a great number of individuals are being extracted before they have reproduced to replenish the populations. Marine resources managers around the world, have the challenge to revise and, if necessary, adapt the existing management strategies. They need to take in account, the species population dynamics and at the same time pursue the aim of maintaining a profitable and sustainable fishery. Moreover, they have to effectively evaluate potential outcomes of alternative measures, and communicate feasible recommendations in a local and regional scale. One way of exploring the effect of the current management strategies and their possible adaptations, is by means of simulation models. This study examines the effect of current and potential fisheries management scenarios on the population dynamics of the green spiny lobster (*P. gracilis*) using an individual based population viability analysis.

The life cycle of the green spiny lobster, as other lobsters, is characterized by a long pelagic larval stage of around nine months in comparison to the larval life of clawed lobsters which is usually of 20 to 30 days. After traveling for thousands of kilometers with the major superficial and underwater currents, young spiny lobsters, settle in small crevices at shallow coasts. This larval period allows broad dispersal and interconnection to other populations in the ETP. Pollock (1993) says that this can be seen as if all local populations of the green spiny lobster would contribute with larvae to a common oceanic supply and their dispersal pathways depend on the water currents system. Therefore, recruitment, or the addition of new individuals to each of the local populations, depends in part on the production of eggs of other interconnected populations and the local carrying capacities. Thus, at an amply large scale, groups of local populations act as one closed population (Caley et al., 1996). The relative importance of the different local populations to the maintenance of the group of populations is, in this case, unknown.

Common fisheries management practices in the ETP include the prohibition of exploiting egged females and a minimum landing size (MLS) which aims to ensure the reproduction of adult individuals before being fished. Additionally, some countries manage effort (number of boats, number of fishermen, fishing seasons and fishing quotas), and type of fishing gear (División de Pesquerías, 2012; Guzmán et al., 2008b; Ministerio de Comercio Exterior Industrialización y Pesca, 2001; Naranjo Madrigal, 2011a; Secretaría de Agricultura, Ganadería, Desarrollo Rural, 2007). The aim of these fisheries management strategies is to maintain populations at their maximum production and with a positive growth rate. MLS regulations are established by each country's authority. In Costa Rica and Mexico MLS are similar: 80 mm carapace length (CL) and 82 mm CL, respectively. Panama has the smallest MLS with 60 mm CL or 120 mm tail length and Ecuador the largest with 260 mm total body length or 150 mm tail length (around 90 mm CL). The rest of the countries in the ETP where *P. gracilis* inhabits have no specific fishing regulations for this spiny lobster species.

Fisheries management regulations, such as MLS, and their potential effects have been established using estimates of the size of onset maturity (SOM) and yield-per-recruit assessments. SOM is the size at which a proportion of 50% of the females in a population have attained sexual maturity. SOM for the same species may vary at geographical scales, due to changing environmental conditions such as temperature, due to density-dependence, and due to fishing pressure (Ellis et al., 2015; Green et al., 2014; Queirós et al., 2013).The maximum yield-per-recruit returns the best size of individuals to

harvest. At this size, the interaction of growth, natural mortality and fisheries mortality produce the highest yield (Cruz, 2002; Gayanilo & Pauly, 1997; Sparre & Venema, 1998). A limitation of yield-per-recruit models is that these don't regard possible changes in recruitment and reproduction as a result of shifts in the population size and environmental variations. They don't include density-dependent mechanisms and many times are not corroborated by simulation models (Gayanilo & Pauly, 1997; Sparre & Venema, 1998). Through the use of a population viability analysis some of these aspects are addressed and explored.

Ecological models such as population viability analysis (PVA) are commonly used to assess the conservation status of small populations. PVA models are able to characterize and predict variations in the abundance of a species over time and are based on population parameters that allow to calculate the population growth. Here, I use an individual based population viability analysis model to study the effect of the current and potential management regulations on the green spiny lobster population in the ETP. Individual based models (IBM) allow to account for the variability of the individuals' attributes and behaviors, to simulate populations or systems of populations (Berger et al., 2008; DeAngelis & Grimm, 2014b; DeAngelis & Mooij, 2005).

Previous lobster IBMs have explored juvenile behavior and reproducing aggregations of spiny lobster (*Panulirus argus*, Butler 2003), recruitment of spiny lobster in degraded nursery habitats (*Panulirus argus*, Butler at al., 2005), larval dispersal of American lobster coupled with biophysical dynamics (*Homarus americanus*, Incze et al., 2010), climate effects on mortality-based biological reference points for Pronghorn spiny lobster (*Panulirus penicillatus*, Chang et al., 2011), and the effect of alternative harvesting practices on the European lobster (*Homarus gammarus*, Sundelöf et al., 2015).

The individual based population viability analysis model presented in this study is called the B52 Spiny Lobster and will be referred throughout the text as the B52 model. The B52 model was implemented in Vortex 10 (Lacy & Pollak, 2014), a free computer program specially designed for conducting population viability analysis. Vortex 10 was developed by the Chicago Zoological Society and is supported by the IUCN Species Survival Commission's Conservation Breeding Specialist Group. Vortex 10 is a ready-to-use population viability analysis software, which allows users to enter the species life cycle's parameter values and functions describing processes to simulate population dynamics at various levels of complexity. The Vortex 10 developing team and users around the world are constantly revising and improving the program. Vortex has been used by private and governmental environmental agencies to evaluate the conservation status and risk of extinction of small populations (see for example Naveda-Rodríguez et al., 2016; Nilsson, 2013; Desbiez et al., 2012; Ebenhard, 2000; Heinsohn et al., 2004; Hosack et al., 2002; Jaric et al., 2010; Manlik et al., 2016; Marshall et al., 2009; Penn et al., 2000; Pergams et al., 2000; Rivera, 2014), to evaluate the effect of management actions including recovery strategies in the case of endangered species (see for example Carroll et al., 2014; King et al., 2013; Licht, 2014, 2017; Licht et al., 2017), and to assess strategies for controlling population sizes in the case of introduced invasive species (see for example Ballou et al., 2008, Micheletti, *in prep.*).

In the ETP, confronted with the decrease of fisheries yield and higher proportions of small individuals, the revision and adaptation of spiny lobster fisheries regulations is impending. Some researchers suggest to enlarge the MLS in order to recover the population (Guzmán et al., 2008), whereas others suggest to decrease the MLS to eliminate illegal fishing and increase the yield and thus the benefit to small scale artisanal fishermen (Murillo et al., 2013). Sundelöf, et al. (2015), showed that for the European lobster the protection of egged females conserves the population and maximizes the yield. Small MLS produces high yield at low fishing effort and large MLS secures productivity even at high fishing effort. My hypothesis is that if current regulations would have been applied in the first place,

the green spiny lobster populations in the ETP would be in a good shape and would maintain a sustainable long-lasting fishery. Furthermore, protecting egged females should increase the number of individuals in the reproductive stock and therefore the population and the catch; and maintaining a large MLS should allow to avoid fishing individuals smaller than that optimal size and thus protect the population from growth overfishing.

In this study, I explore five current fisheries management scenarios to investigate how important is to protect juvenile lobsters, the enforcement of a MLS and the protection of egged females, with respect to the population size, the production of offspring, and the catch. I investigate how sensitive is the B52 model to alternative mortality values at different ages and to varying percentages of breeding individuals availability. Finally, I explored the effect of varying MLS under different fishing effort and the impact of establishing an MLS below the size at sexual maturity. As a case study, I use the green spiny lobster *P. gracilis* in the ETP. The B52 model was parameterized using empirical data from Ecuador and values from the literature.

2.2 METHODS

2.2.1 The species: green spiny lobster (*Panulirus gracilis*)

The green spiny lobster was selected for this study because it is the most widely distributed in the Eastern Tropical Pacific. *P. gracilis* inhabits the eastern Pacific, from Baja California, Mexico to northern Peru, and the Galapagos islands. It occupies coasts with water depths between 0 to 40m, among rocks, in cracks and crevices (Briones-Fourzán & Lozano-Alvarez, 1992; Holthuis, 1991; Holthuis & Loesch, 1967). It is also found over sandy areas with gravel since it tolerates a wide range of water turbidity (Briones et al., 1981; Lozano et al., 1982; Pérez-González et al., 1992).

P. gracilis larvae, called *Phyllosoma*, go through a metamorphosis of eleven larval stages before settling in small crevices at shallow coasts. Larvae are able to travel for thousands of kilometers depending on the major superficial and underwater currents. As an example of their widespread movement, Cobb & Wang (1985) found *P. gracilis* larvae 4000 km away from any possible source. Johnson (1971) found high concentrations of *P. gracilis* between Galapagos, mainland Ecuador and Costa Rica, and around 2500 km to the West of Galapagos. This indicates that the persistence of spiny lobster populations at one locality does not exclusively depend on the local reproduction, and that populations in the region are interconnected. However, the relative importance of each of the breeding populations is unknown.

For a detailed description of the species see Section 1.2 in Chapter 1.

2.2.2 Data

2.2.2.1 Empirical data measured during this study

Parameter values and value ranges were calculated from empirical data from the fisheries monitoring of a small scale fishery at the northern coast of mainland Ecuador, in Cape San Francisco, at the Galera-San Francisco Marine Reserve. The resulting estimated values were compared and complemented with empirical data from the Galapagos Marine Reserve and published literature from the Eastern Tropical Pacific.

For a detailed description of data collection see section 1.5 in Chapter 1.

2.2.2.2 Literature survey to complete the data set

I searched for all available publications about the green spiny lobster *P. gracilis*. I considered peer reviewed international journals, publications in local scientific journals, as well as governmental and non-governmental organizations' reports, and thesis manuscripts. I selected those studies that presented age at size, size at weight, length-length relationships, size at maturity (SOM), natural mortality and offspring size, as well as management regulations such as MLS values.

For a detailed description of the literature survey see section 1.5 in Chapter 1.

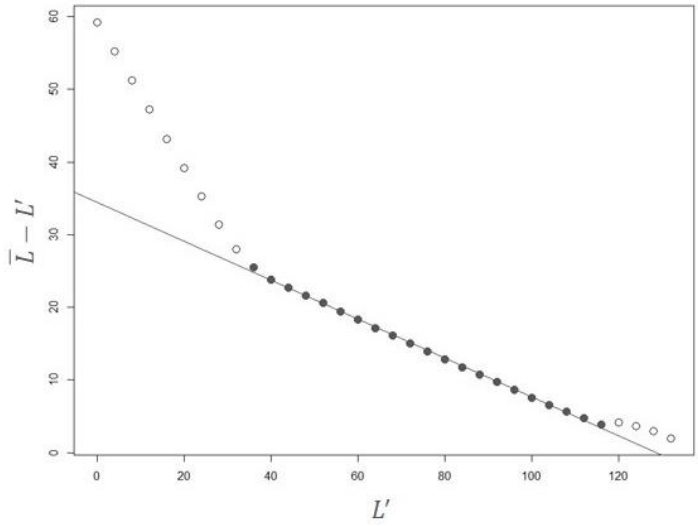
2.2.3 Data transformation

Individuals in Vortex 10 are characterized by age, and not by size as it is common in fisheries monitoring data. Therefore, data given in sizes in the literature (MLS, SOM, mortality at size, fertility at size) were transformed to their equivalent in years. Transformations were based on the existing growth parameters published in the selected studies and the values calculated from the empirical length-frequency data. Age at different sizes were then estimated using the von Bertalanffy growth function (VBGF) for females and males separately (Bertalanffy, 1957):

$$EL_t = L_\infty\left(1 - e^{-K(t-t_0)}\right),$$

where EL is the expected average length at time t, and is defined by three growth parameters: L_∞ which is the asymptote for the model of average length-at-age, K which is the body growth coefficient measured in time ($years^{-1}$) and determines how fast the spiny lobster approaches its asymptotic length (L_∞), and t_0 which is the age at which the size of the organism is zero. Since this is biologically impossible, this constant is regarded as artificial, and is used only to define the x-intercept of the growth curve (Beverton, 1954; Beverton & Holt, 1957). In that way, in this study, I assumed $t_0 = 0$. Separate analyses were chosen to generate L_∞ and K because of their inter-dependence (one quantity entails the other). In all studies, L_∞ and K where estimated using the Powell-Wetherall plot (Powell, 1979; Wetherall, 1986) and the Shepherd's Length Composition Analysis (SLCA) method, respectively. The Powell-Wetherall plot shows the relation of the mean length ($\overline{L}$) of all individuals above the cut-off length (L') and L' (Figure 2.1). L' indicates the size of the smallest fully recruited individuals for each size class. This returns a linear regression where the intercept a corresponds to L_∞. This method assumes that there is a linear decrease in growth with increased length, in other words it follows the VBGF. A further assumption is that the population sampled is in steady-state (i.e. in equilibrium, the population doesn't grow without limit, nor die out) with a constant exponential mortality. Finally, this method assumes that there are no variations in the fishery's selectivity pattern and that recruitment is constant (Gayanilo & Pauly, 1997; Sparre & Venema, 1998; Wetherall, 1986).

The parameter K was estimated using the SLCA method in the software FISAT II (Gayanilo et al., 2005) which assumes no seasonal oscillations in growth. This method provides the option to search for the best value of K for a fixed value of L_∞ by using a score function S. S evaluates the goodness of fit of the length frequency distribution for each combination of parameter values. The selected K value is the one that reaches the highest score and thus, is assumed to be the more consistent with the data (Gayanilo et al., 2005; Gayanilo & Pauly, 1997).



$$\overline{L} - L' = a + bL'$$

where

$$\overline{L} = \left(\frac{L_\infty + L'}{1 + (Z/K)}\right)$$

$$L_\infty = -a/b$$

$$Z/K = -(1 + b)/b$$

Figure 2.1. The Powell-Wetherall plot shows the relation of the mean length ($\overline{L}$) of a sample minus the smallest length group fully recruited by the fishing gear (cut-off length L') against L'. The regression analysis is carried out using the filled dots which represent the minimum size that an individual reached before being fully recruited to the fishery.

In fisheries science, yield is generally expressed as the catch in weight. If not provided, weight can be calculated by means of linear and non-linear equations that relate a measure of size with a measure of weight. Spiny lobsters, as other crustaceans, exhibit sexual dimorphism. In other words, sexually mature females can develop longer and heavier tails than males of the same size (Loesch & Lopez, 1966; Figueroa & Mero, 2013; Hearn, 2005; Murillo Posada et al., 2013; Naranjo Madrigal, 2011). Hence, size-weight equations are more accurate if they are estimated for males and females separately. Furthermore, such relations may also vary in space and over time (Briones-Fourzán & Lozano-Álvarez, 2003; Newman & Pollack, 1974). In this study, the results of harvesting lobsters in the different scenarios, are presented as catch in number of individuals and not as yield.

2.2.4 The B52 Spiny Lobster model

The B52 model is an individual based population viability analysis model implemented in Vortex 10 (R.C. Lacy & Pollak, 2014). Vortex 10 is a free computer program developed by the Chicago Zoological Society and supported by the IUCN Species Survival Commission's Conservation Breeding Specialist Group. Vortex 10 allows to simulate the effect of deterministic forces on the population dynamics of a species, as well as stochastic environmental, genetic, and demographic events. Population dynamics are modelled as discrete, sequential events that occur with probabilities that are random variables according to user defined distributions (Robert C. Lacy, Miller, & Traylor-Holzer, 2017). Vortex 10 is an individual based model thus, it determines for each individual if any of the life cycle events occur and keeps a memory of the characteristics of each animal. The B52 model was parameterized for the green spiny lobster (*P. gracilis*), using published literature and empirical data.

The ODD (Overview, Design concepts, Details) protocol is used to describe the B52 model in the text below (Grimm et al., 2006, 2010).

2.2.4.1 Overview

Purpose

The aim of the B52 model is to investigate how the current management regulations and potential alternatives impact on the population size, offspring production and catch of an exploited population of *P. gracilis*.

Entities, state variables and scales

Entities are individual spiny lobsters characterized by age (years) and sex. Ages are estimated using the age-length relationship by Von Bertalanffy. Males and females turn adults at three years old when they start breeding.

Adult females are characterized by two age-dependent state variables. The first one determines the number of times per year that a lobster will carry and release eggs (number of broods per year). The second one determines the number of eggs per brood that enter the population (number of offspring per brood).

The B52 model is spatially implicit. It represents one population of *P. gracilis* with most parameter values calculated for Ecuador. Each time step represents one year in the model. Simulations are run for 100 years to allow the population stabilize before introducing the fishing scenarios after 50 years.

Process overview and scheduling

The events of the life history of the spiny lobster included in the B52 model occur at each time step (year). The sequence of events is the same every year. Figure 2.2 presents the processes included in the B52 model, in the sequence suggested by Vortex 10. Vortex 10 offers the possibility to include additional processes that were not implemented in the B52 model, such as dispersal and genetic information.

Breed. Females sexually mature will successfully produce offspring considering the probability set in the percentage of breeding females per year. The number of broods per year and the size of each brood is determined by the age of each individual adult female. In this study, I adapted for Vortex 10 an age-specific function for the number of broods and the offspring size per year per individual. It is assumed that a high percentage (90%) of the adult males are available for reproducing.

Mortality is given as a yearly percentage per age class for each sex. Values are assumed to consider natural mortality only. Total mortality includes the mortality dependent on density (regulated by the carrying capacity) and fishing mortality represented in by the harvest functions.

Harvest occurs each year starting in year 50 after an initial period of 50 years to stabilize the population dynamics. In the B52 model, four scenarios are simulated according to different harvesting regimes and one scenario without harvest (Table 2.1). Simulated scenarios represent the most common harvest strategies for the green spiny lobster in the Eastern Tropical Pacific. The key parameters to characterize current practices are minimum landing size (MLS) and fishing mortality represented as the proportion of the population extracted at different age classes.

In the B52 model, the ideal scenario which applies all management regulations was created: the prohibition of fishing individuals smaller than the MLS and egged females. I called this scenario “legal fishing”. Two scenarios which explore independently the effect of disrespecting those regulations: “fishing juveniles” and “fishing egged females”. One scenario depicts the current situation taking place in most locations with no control and no respect for any regulation. This is the “worst case” scenario. Finally, a null scenario with no fishing was modelled. Scenarios and their descriptions are presented in Table 2.1. After an initial period of 50 years to stabilize population dynamics, 50 more years are used to explore all management scenarios.

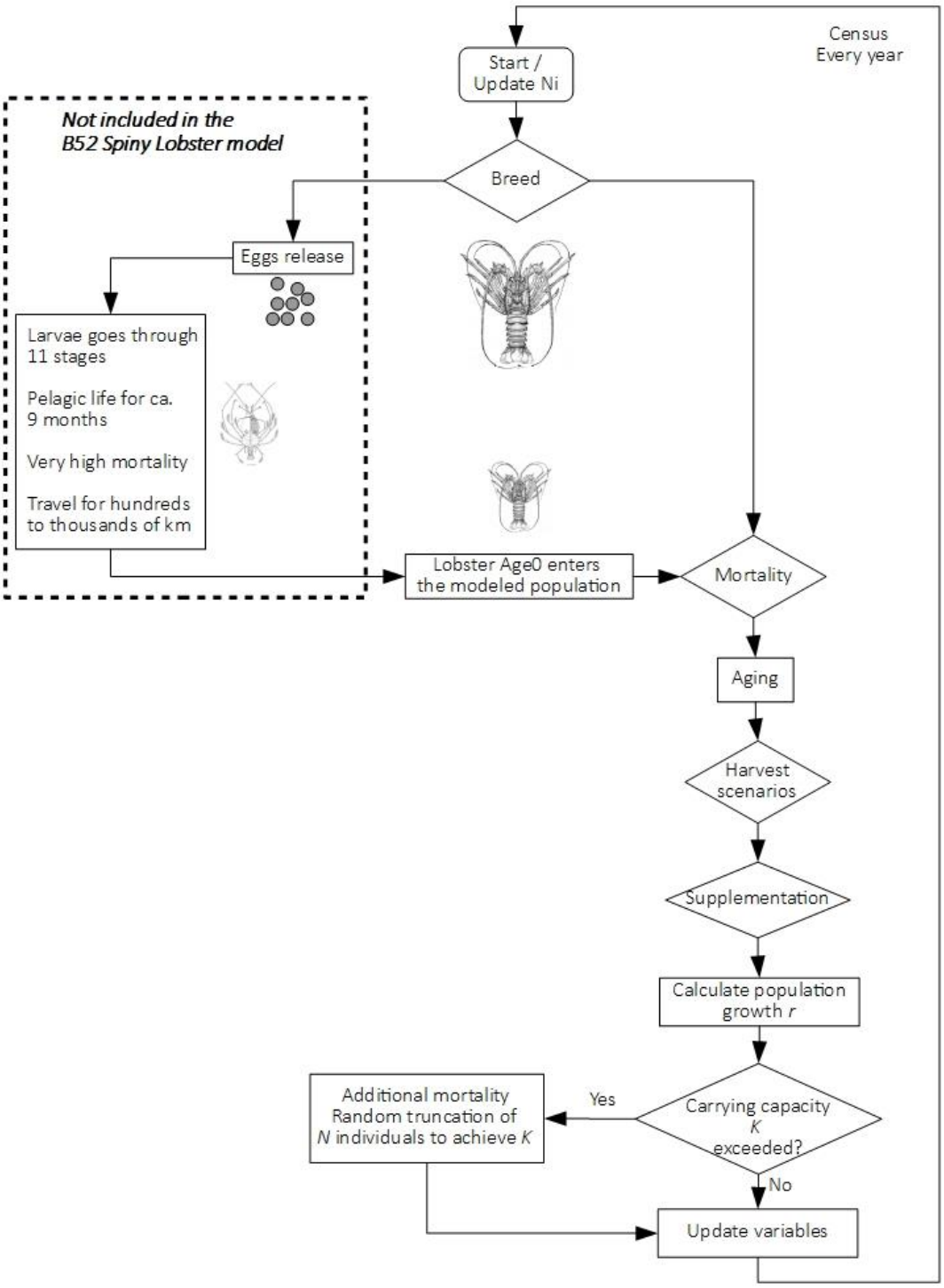


Figure 2.2. Scheduling of events in Vortex 10. The pelagic larval phase is not included in the life-cycle events modeled in this study. The percentage of individuals breeding of defined for females and males separately. The number of juvenile lobsters at Age0 that enter the population is dependent on the age of the lobsters reproducing. Larger females produce more viable eggs. Natural mortality takes place according to age dependent percentages. Juveniles have a higher mortality than adults. Four harvest scenarios and a "no fishing" scenario were modelled in this study (see Table 2.1). Supplementation refers to external input of juveniles of Age0 (independent of the state of the local adult population). Larvae sketch is from Johnson (1956) and the spiny lobster illustration is from Holthuis (1991).

Table 2.1. Scenarios modeled in Vortex 10 represent the current and most common harvesting strategies.

Scenario	Description
No fishing	No individuals are harvested from the population.
Legal fishing	Egged females and individuals smaller than the legal minimum landing size (MLS) 26 cm total length (equivalent to 4 years old) are not fished. The rest of the individuals have a determined probability to be fished.
Fishing juveniles	Individuals of both sexes and all ages starting from one are fished with a certain probability. Egged females aren't fished.
Fishing egged females	Egged females and individuals at or larger than the MLS of 26 cm total length (equivalent to 4 years old) are fished with a determined probability. No individuals below the MLS are fished.
Worst case	Egged females, undersized individuals, and individuals at or larger the MLS are fished indistinct of their sex and age.

2.2.4.2 Design concepts

Basic principles, management of fisheries focuses on maximizing the catch and avoiding overfishing. The B52 model was designed to better understand the effect of current harvesting scenarios on population size, the catch of lobsters, and the production of offspring. In this study, catch is presented in number of individuals and not as yield, which is the catch expressed in weight. This is because the model was not designed to return the age structure of the harvested individuals.

Emergence, catch in number of individuals, offspring, as well as probability of extinction, long term growth rate and size structure emerge from age-dependent natural mortality, age-dependent reproduction, harvest scenarios (effort), and minimum landing size (MLS).

Interaction, only implicit, assuming density dependent reproduction, harvesting, and recruitment.

Stochasticity, reproductive rates such as the probability that an adult female will successfully produce offspring in a given year, percentage of available males to reproduce, the number of broods and the brood size, as well as mortality rates per age, will produce variability among individuals and in population outcomes such as age structure, offspring produced, and catch. The probability value by which an event will happen to an individual, is randomly selected from a certain distribution with the specified mean and standard deviation. Standard deviations represent a random variation due to environmental variability.

Observations, for each scenario modelled and sensitivity tests, the number of individuals present in the population at the end of each year, the number of individuals harvested, and the size of the offspring are recorded.

2.2.4.3 Details

Initialization

The number of individuals in the population is unknown. The B52 model was tested with different initial number of individuals and a stable age distribution. In all cases, the B52 model was run for 50 years without harvest to an equilibrium state before modelling the scenarios for another 50 years each. At a carrying capacity estimated at 10000 individuals, the initial population size was 8648 individuals. Detailed information and parameter values are presented in Table 2.2.

Table 2.2. Description of parameters and their values in the B52 model.

Parameter	Description	Value	SD	Comments	Units	Source
Age of first offspring	This is known for females. It was assumed that it is the same for both sexes	3	-	In Mexico (Briones-Fourzan, 2014) and Galapagos (Reck, 1983), the age at first maturity is 2	Years old	Empirical data Luna, this study (Figure2.3)
MLS / age at first capture	Minimum Landing Size. This is established by each country. Here, the MLS in Ecuador: 26cm of total length is used as reference	4	-	In Mexico (Briones-Fourzan, 2014) and Galapagos (Reck, 1983), the MLS would be attained between 2-3 years old	Years old	Empirical data Luna, this study (Figure2.3)
Maximum age of reproduction		12	-		Years old	Naranjo Madrigal, 2012
Number of broods per year	Times per year *P. gracilis* can bear eggs is age dependent.	Maximum 4 at age >= 5 3 broods at age 4 2 broods at age 3			Number of times	Briones-Fourzan, 2014; Mero-Del Valle et al., 2015; Naranjo Madrigal, 2012; Quackenbush, 1994
Females breeding	30		10		Percentage	(Correa et al., 1994; Figueroa & Mero, 2013; Reck, 1983; Villón et al., 2000)
Mortality rate per sex and age class (females)	Mortality per sex and age class for 25°C mean SST in the Galera-San Francisco Marine Reserve	Age0 = 50 Age >= 1 = 20	Age0=10 Age >= 1 = 3	Assumed the same mortality for males and females. Calculated difference was only of 2%.	Percentage	Empirical data Luna, this study Empirical formula from (Cruz, 2002)

Input

No external input is included.

Submodels

Breeding

In the B52 model, the implemented function allows for older individuals to bear more broods per year than younger ones. Females that just start reproducing at age 3, will have two broods per year, whereas larger, and older lobsters, are able to have four broods per year:

= (2*(A=3)) + (3*(A=4)) + (4*(A>=5)), where A is age.

The size of the brood, meaning the number of eggs per brood per female, is related to the individual's age. Younger and smaller lobsters bear smaller eggs. The fitness and the probability to survive is decreased in smaller eggs (Moland et al., 2010; Sundelöf et al., 2015). Lyons et al. (1981) and Quackenbush (1994) documented that the largest lobsters in the population can have from five up to nine times more successful larvae that the smallest reproducing individuals. The B52 model incorporates in the simulation the dynamics of the surviving young lobsters and not the dynamics of

the individual larvae. This was implemented by considering only the number of individuals that survive. In the B52 model, this was implemented as follows:

= (2*(A=3)) + (4*(A=4)) + (8*(A=5)) + (10*(A>=6)), where A is age.

In Vortex 10, these functions are specified and recorded in so called individual and population state variables. These are different from the state variables defined in the ODD, since those in Vortex 10 can be calculated from the actual state variables of the individuals.

Ageing
Every year all extant individuals turn one year older. Lobsters older than 3 years become reproductive until they reach their maximum lifespan of 12 years. Juveniles have Age = 0, subadults are 1 and 2 years old and all individuals equal and over 3 years old are adults.

Harvest
Population was harvested after 50 years of no extraction and until the last year of the simulation. Harvesting events took place every year. Depending on the harvest scenario, percentages of the population at age were exploited.

Population's growth rate (r)
The Population's growth rate (*r*) is reported for the years without harvest, for the years with harvest and supplementation, and for the average across all years. If the population reaches the carrying capacity K, *r* is calculated before the truncation (mortality of excess individuals).

Carrying capacity (K)
Vortex 10 implements carrying capacity as a probabilistic truncation across all age classes when *K* is exceeded at the end of the year.

2.2.5 Sensitivity tests

The relative importance of the parameters within the B52 model was tested using a local and a global sensitivity analyses. The local analysis was made using three scenarios: “no fishing”, “legal fishing” and “fishing egged females”. Base parameter values for mortality at different ages and the percentage of breeding females and males, were varied one-at-a-time in plus and minus 5 to 10%, while all other parameter values were maintained unchanged.

In a global sensitivity analysis, MLS and fishing effort were varied to explore their combined effect on the population size, the catch, and the offspring produced. The analysis was performed using Latin Hypercube Sampling (LHS) which is implemented in Vortex 10 sensitivity test options. The range of values for each parameter is defined, as well as the number of samples that should be taken from that range. Vortex 10 divides evenly the parameter space and values are sampled randomly from each parameter. This is repeated a defined number of times and each value from each parameter is tested once against each other.

2.3 RESULTS

2.3.1 Data transformation of the empirical data

In this study, I used the empirical data from the Galera-San Francisco Marine Reserve to estimate the size at age. I took as reference the MLS regulation for Ecuador which is of 26 cm total length (around 78 – 82 mm CL). Estimations in this study suggest that the age at first reproduction for females and males of *P. gracilis* is 3 years. The MLS is achieved when lobsters are between 4 to 5 years old. The analysis of the literature revealed that values for the asymptotic length L_∞ and the curvature parameter K differ among studies of *P. gracilis* in the ETP (Figure 2.3 and Table A2.1 in Annex 1). Figure 2.3 shows an example of the magnitude of the differences among the growth curves estimated for female *P. gracilis* in the region. In contrast to Mainland Ecuador (Luna, this study), in Galapagos (Reck, 1983) and Costa Rica (Naranjo Madrigal, 2011b), SOM and MLS are achieved at a younger age between 2 and 3 years old (Figure 2.3).

Additionally to growth, SOM, and fertility functions for the same species in the region, are different among places and over time (Table 2.3). Moreover, they are expressed taking in account different parts of the lobster body in the various studies. For instance, studies conducted in localities in North and Central America, lengths refer commonly to the carapace, whereas in Ecuador lengths refer to two measurements - the tail and the total body. Generally, morphological models that describe a body measure in relation to another, like the length-length and the weight at length relationships, are used to calculate missing measures. Nevertheless, I observed that lobster body measures were not taken in a standardized way in all localities studied in the ETP, and therefore, such equations are not directly comparable among each other making it difficult to form a regional perspective.

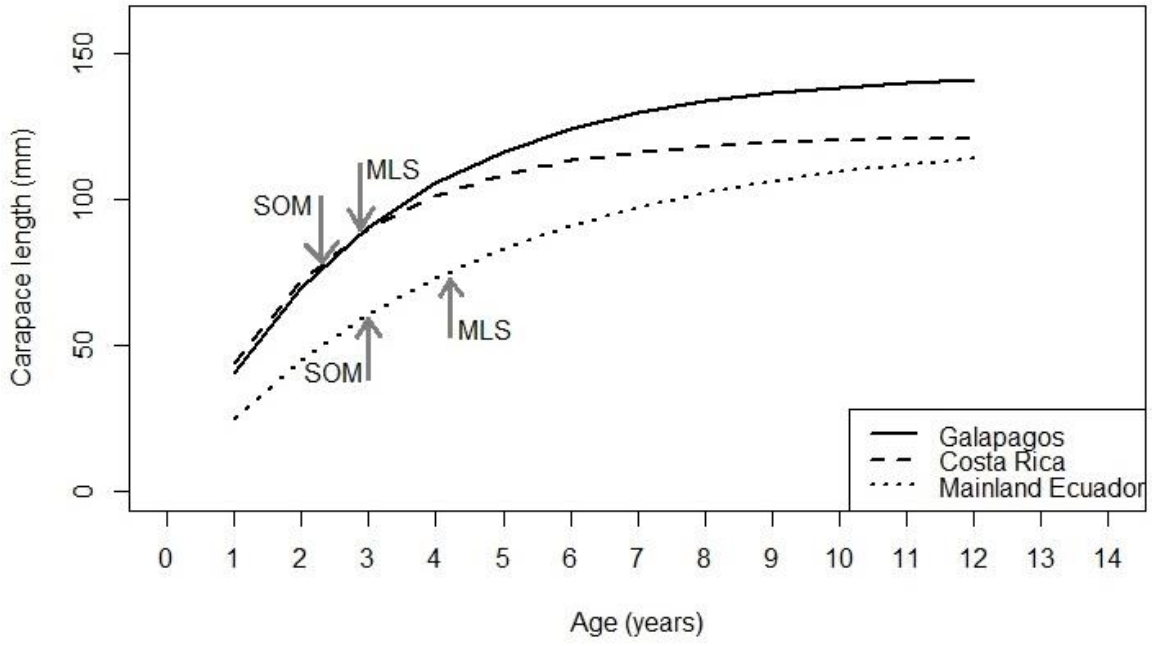


Figure 2.3. Growth curves for female green spiny lobsters in Galapagos (Reck, 1983), Costa Rica (Naranjo Madrigal, 2011b), and Mainland Ecuador (this study). Growth parameter values are presented in Table A2.1 in Annex 1. Arrows show the age in years at the size of onset maturity (SOM) and the minimum landing size (MLS).

2.3.2 Sensitivity Analyses

The local sensitivity analysis scanning a variation of ± 5 and 10% in the B52 model parameters, shows that the population size in scenarios with fishing impact are more sensitive to changes in mortality and percentage of breeding individuals (Table 2.4). Particularly, increasing juvenile mortality reduces the population size and the catch. Increasing adult mortality negatively affects population size, offspring production, and catch. The production of offspring in the "no fishing" scenario is larger with a higher mortality of juveniles and subadults and, as expected, decreases with a higher mortality of adults. However, offspring production increases almost in double when the percentage of breeding females decreases in 10%. This counterintuitive result occurs only in the "no fishing" scenario, where the population is at the carrying capacity. In the "legal fishing" and "fishing egged females" scenarios, a reduction in the percentage of breeding females, reduces the offspring and, increasing the percentage of breeding females, lessens the offspring as well. These results, in combination to the decrease of the population size when reducing the percentage of breeding females, suggests that at low density the production of offspring is reduced. In the same way, the offspring production drops off when the population is large (Table 2.4). The B52 model was not sensitive to a variation in the percentage of breeding males (5 to 70%), showing no significant effect on the population size, the offspring production, or the catch.

Table 2.3. Available fecundity functions and size of onset of sexual maturity (SOM) from different studies in the ETP taken at various years. SOM is given as the carapace length in mm.

Study	Site	Year sampled	Number of females sampled	SOM (CLmm)	Fecundity function
Briones and Lozano (1977)	Ziguantanejo, Mexico	1976-1977	-	75	
Briones and Lozano (1992)	Ixtapa, Mexico	1979-1980	-	75	
Briones (2014)	Ziguantanejo, Mexico				$\text{Egg number}^3 = 9.8651 * length^{2.4634}$
Perez-Gonzalez et al. (2012)	Sinaloa, Mexico		259		$\text{Egg number}^3 = 0.6803 * length^{3.1007}$
CENDEPESCA (2012)	Playas Negras, El Salvador	2011-2012	-	54	
Naranjo (2012)	Playa Lagarto, Costa Rica	2007-2008	357	75	
Guzman et al. (2008)	Las Perlas, Panama	2006	69	84	
Guzman et al. (2008)	Coiba, Panama	2007	297	84	
Toral et al. (2002)	various sites Galapagos, Ecuador	1998-2000	8	88	$\text{Egg number}^3 = 29.421 * length^{2.9388}$
Loesch and Lopez (1966)	various sites mainland, Ecuador	1962-1963	64	89,5	
Mero et al. (2015)	Santa Rosa, Ecuador	2012	273	83	$\text{Egg number}^3 = 16.231 * length - 971.24$
Murillo et al. (2013)	Anconcito, Ecuador	2013	337	80	
This study	Galera San Francisco Marine Reserve, Ecuador	2012	371	60	

2.3.3 Ground-truth: empirical data and B52 model results

A comparison of the resulting modelled population's age structure to the age distribution of field data, represented the sampled populations reasonably. The empirical data available from the Galera-San Francisco Marine Reserve, as an example of an over-exploited population (Figure 2.4A), were compared to the modelled results of the "worst case" scenario (Figure 2.4B), where no regulations are enforced. The B52 model captures the steep variations in the proportion of juveniles and adults from year to year. In the worst case scenario, juveniles are extracted causing an abrupt decrease in the size of the population (N) from one year to another.

It was not possible to contrast the modelled "legal fishing" scenario to empirical data from for example the Galapagos Marine Reserve, since fisheries independent data for the green spiny lobster in Galapagos are scarce. Therefore, a comparison of the population structure of the modelled scenario to the empirical data of a legally fished location is not accurate. The empirical data show that the fished and sampled green spiny lobsters in Galapagos between 1977 and 2005, had a percentage of adult individuals between 95 and 100%. Thus, this is only showing that the MLS regulation is enforced and the fishery is mainly composed by adult individuals. In this case, it is necessary to gather fishery independent data that monitor a broader range of lobster ages and sizes, including juveniles.

Table 2.4. Percent change in the B52 model output population size, offspring production and yield given the percent change in the parameters mortality at age and percentage of breeding females per year. The analysis was made at three scenarios: "no fishing", "legal fishing" and "fishing egged". Base parameter values were varied in plus and minus 5 to 10%. Base values used in the B52 model are a juvenile mortality of 50%, a subadult mortality of 20%, an adult mortality of 20%, and percentage of breeding females of 30%.

	Population size					Offspring					Catch				
No fishing Scenario	**-10%**	**-5%**	**0**	**5%**	**10%**	**-10%**	**-5%**	**0**	**5%**	**10%**					
Juvenile mortality	-0.9053	-0.62662	0	-0.34523	-1.61695	**-17.1911**	**-9.95918**	0	**10.35117**	**22.0685**					
Subadult mortality	-0.16517	-0.60071	0	-0.61157	-1.33193	**-9.14289**	**-5.83324**	0	4.685928	8.942538					
Adult mortality	0.593475	0.690877	0	0.130037	0.329474	**23.20351**	**12.15802**	0	**-10.5345**	**-20.9357**					
Percentage of breeding female	-0.43118	-0.89984	0	0.190275	-0.07027	**45.1587**	**18.16847**	0	**-14.1304**	**-24.3867**					
Legal fishing Scenario	**-10%**	**-5%**	**0**	**5%**	**10%**	**-10%**	**-5%**	**0**	**5%**	**10%**	**-10%**	**-5%**	**0**	**5%**	**10%**
Juvenile mortality	6.678561	4.332303	0	-9.21582	**-23.763**	**-10.6044**	-5.10449	0	0.60331	-7.04978	2.518271	1.881221	0	-5.01097	**-15.3648**
Subadult mortality	5.379776	2.497965	0	-3.46604	**-10.7157**	0.308502	0.24922	0	-2.11351	-6.74089	6.241547	2.268948	0	-5.88421	**-14.9546**
Adult mortality	4.524677	2.284092	0	-6.42915	**-17.2979**	**21.42983**	**12.2246**	0	**-13.8727**	**-32.4292**	**22.85139**	**12.55986**	0	**-12.5462**	**-30.529**
Percentage of breeding female	**-48.2984**	**-17.0019**	0	4.661215	6.792277	**-29.2453**	-2.92061	0	**-10.1969**	**-20.1291**	**-38.7273**	**-13.7014**	0	0.057993	-0.14619
Fishing egged Scenario	**-10%**	**-5%**	**0**	**5%**	**10%**	**-10%**	**-5%**	**0**	**5%**	**10%**	**-10%**	**-5%**	**0**	**5%**	**10%**
Juvenile mortality	4.443874	2.254506	0	-4.34487	**-16.7014**	**-13.5476**	-6.72375	0	3.867245	2.336077	2.137193	2.17014	0	-3.14099	**-12.5883**
Subadult mortality	2.979514	2.519875	0	-3.5605	-7.078	-2.77847	-0.49737	0	-0.49669	-0.80015	4.487713	1.54565	0	-5.17641	**-11.2471**
Adult mortality	3.463676	2.009341	0	-4.11621	**-11.4192**	**23.47363**	**10.76338**	0	**-14.0046**	**-28.4051**	**17.4678**	8.361753	0	**-11.5358**	**-24.0276**
Percentage of breeding female	**-42.0577**	**-10.8759**	0	2.437272	4.274341	**-15.0817**	6.34717	0	**-10.4643**	**-20.6384**	**-35.1944**	-7.52582	0	-0.27965	-1.82397

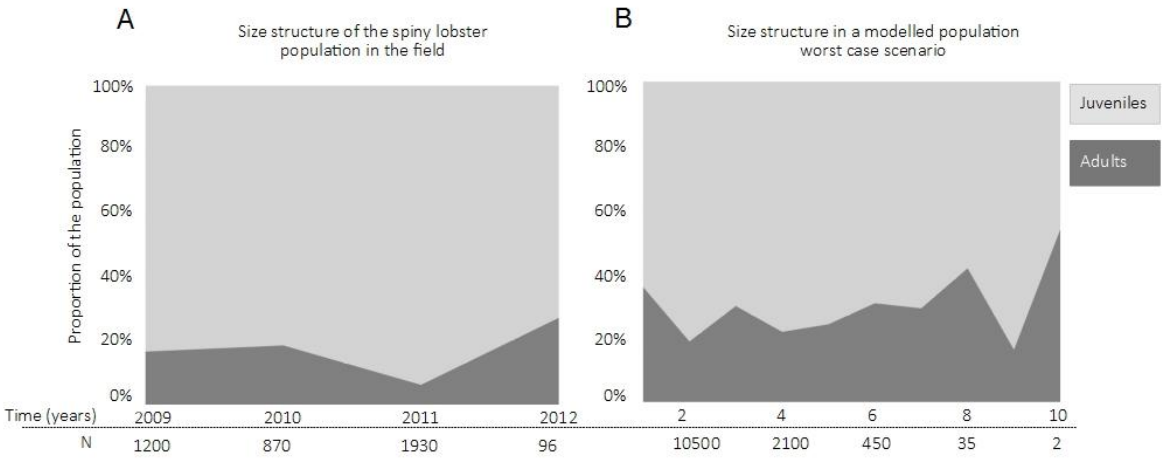


Figure 2.4. Size structure of **A.** an overfished population of *P. gracilis* in the Galera San Francisco Marine Reserve, Ecuador and **B.** a modelled overfished population using the B52 model.

2.3.3 Fisheries management scenarios

Fishing juveniles can lead to population collapse (Figure 2.5A). Adding the extraction of egged females to the juveniles (worst case scenario), will lead to a similar result in an even more accelerated time (Figure 2.5A). In the presence of external input of offspring, "fishing juveniles" and "worst case" scenarios will change the population's probability of extinction from 1 to cero (Figure A2.1A in Annex 2). Additionally, with external input of offspring, their age-distributions may turn from very irregular due to a small number of individuals (Figure 2.6D and 2.6E), to a population with a ratio of adults of only 15 to 18% and thus, with a low production of offspring, especially when extracting egged females (Figure A2.1B in Annex 2).

Extracting egged females reduces the production of offspring in the population. The B52 model suggest that fishing 50% of the available egged females every year, causes steep decline until it reaches a new equilibrium ten years after introducing fishing (Figure 2.5B). At this stage, the females that just became sexually mature and are still below the MLS, maintain the production of offspring in the population. Younger females produce a lower number of broods per year and a smaller successful offspring per brood. In the B52 model, allowing the fishery of egged females doesn't lead to the collapse of the population, but the amount of offspring produced is diminished to one third of the amount of offspring produced in the "legal fishing" and "no fishing" scenarios. The B52 model was not sensitive to the effect of extracting egged females on the population size or the catch. Even more, the resulting population size, when extracting egged females, shows no difference from the "legal fishing" scenario and the "no fishing" scenario (Figure 2.5A). Similarly, the age-structure in the "legal fishing" and the "fishing egged" scenarios, show a proportion of around 20% of adults in the population (Figure 2.6B and 2.6C) and around 18% of adults with external input of offspring. A "no fishing" scenario shows a higher and stable proportion of 30% adults (Figure 2.6A).

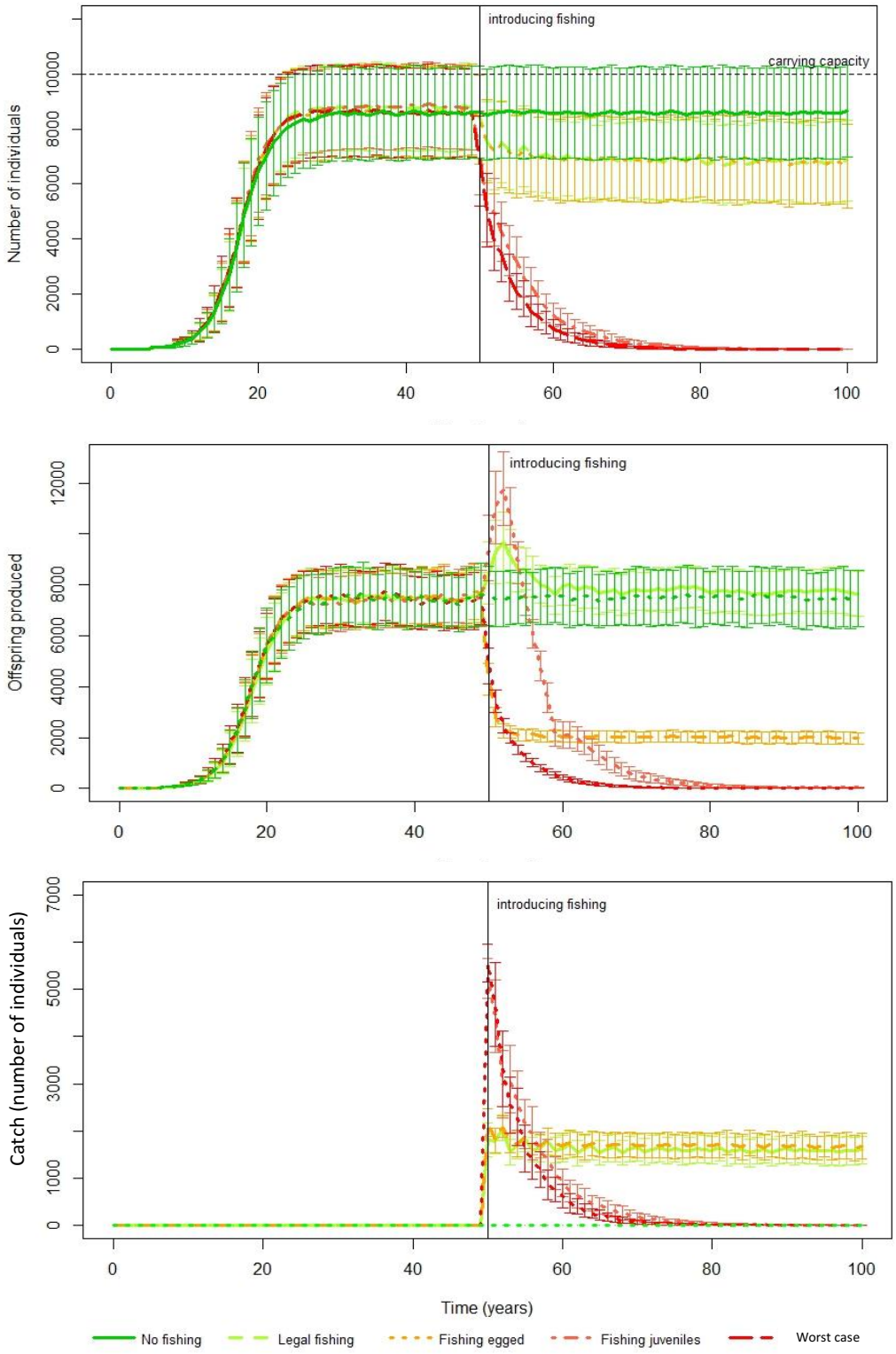


Figure 2.5. Population size (A), offspring produced (B) and catch in number of individuals (C) over time. The simulation runs for 100 years. After the first 50 years when the population has acquired a steady state, five fishing scenarios are introduced. Each of them is represented with a different color. Error bars show standard deviations for each year. Recruitment is dependent on the local population with no external input. The assumed carrying capacity is represented by a horizontal dotted line in A. B and C are not influenced by the carrying capacity.

The B52 model shows that the population at high densities is regulated by the carrying capacity and, at low densities, the regulating factor is the fishery. For example, the “fishing juveniles” and “legal fishing” scenarios, show a peak in the production of offspring during the first years after introducing fishing, with and without input of external offspring (Figure 2.5B and Figure A2.1B in Annex 2). This can be explained by examining the age structure of the population during those years. The population shows that there is a corresponding increase on the proportion of adults in both scenarios causing a higher production of offspring (Figure 2.6B and 2.6D). This can’t be seen in the age structure graphs that include the external input of offspring. The high amount of offspring produced is regulated by the carrying capacity and ten years after introducing the fishery, the “legal fishing” scenario finds an equilibrium in the production of offspring comparable to the “no fishing” strategy. Whereas, the trajectory of the “fishing juveniles”, keeps decreasing in the production of offspring until it reaches a short plateau also ten years after introducing the fishery and then it continues decreasing (Figure 2.5B). The population structure during the years of the plateau, shows again a higher proportion of adults (Figure 2.6D). It also shows abrupt changes from one year to the other due to the small number of individuals in the population. The input of offspring independent of the state of the adult population softens such abrupt changes.

Catch (in number of individuals) is the highest in the scenarios that are more permissive: “fishing juveniles” and “worst case” scenario during the first five years after opening the fishery (Figure 2.5C and Figure A2.1C in Annex 2). In these two scenarios, without the input of external recruitment, catch is reduced to cero within two decades. Fisheries that allow the extraction of egged individuals and the ones that have a moratorium on them, show a stable catch.

2.3.4 Effects of varying MLS and fishing effort

In the global sensitivity analysis, iterating the model with the total range of combinations of effort and MLS, revealed the strategies that maximize the population size, the production of offspring, and the catch in a “legal fishing” scenario (Figure 2.7A,C, and E) and in a scenario in which egged individuals are not protected (Figure 2.7B, D, and F). In all cases, “legal fishing” returns a maximum number of individuals higher than the “fishing egged” scenario. Among the two variables used: fishing effort and MLS, the first has the strongest influence on the spiny lobster population dynamics. Higher levels of fishing effort gradually reduce the population size and the offspring produced, leading to collapse when values approach 1. Furthermore, a fishing effort lower than 0.5, is less important for the production of offspring when protecting the egged females (Figure 2.7C and D).

The catch shows to be influenced by the interaction of fishing effort and MLS in a “legal fishing” scenario (Figure 2.7E). At a small MLS, established at the age of first maturity, a higher effort than 0.8 reduces the catch. A MLS set at four years old, maintains the highest catch at a broad range of fishing effort. When the extraction of egged individuals is allowed, the catch is maximized at a narrow fishing effort range for all MLSs. A lower or higher effort reduces the catch (Figure 2.7F).

A global sensitivity of a scenario that allows the extraction of individuals before they have reached the age at first reproduction shows the highest catch only at high efforts in a scenario with a female moratorium (Figure2.8A). Without an egged female moratorium, the population is more vulnerable to high fishing effort and supports a fishery only with very low effort.

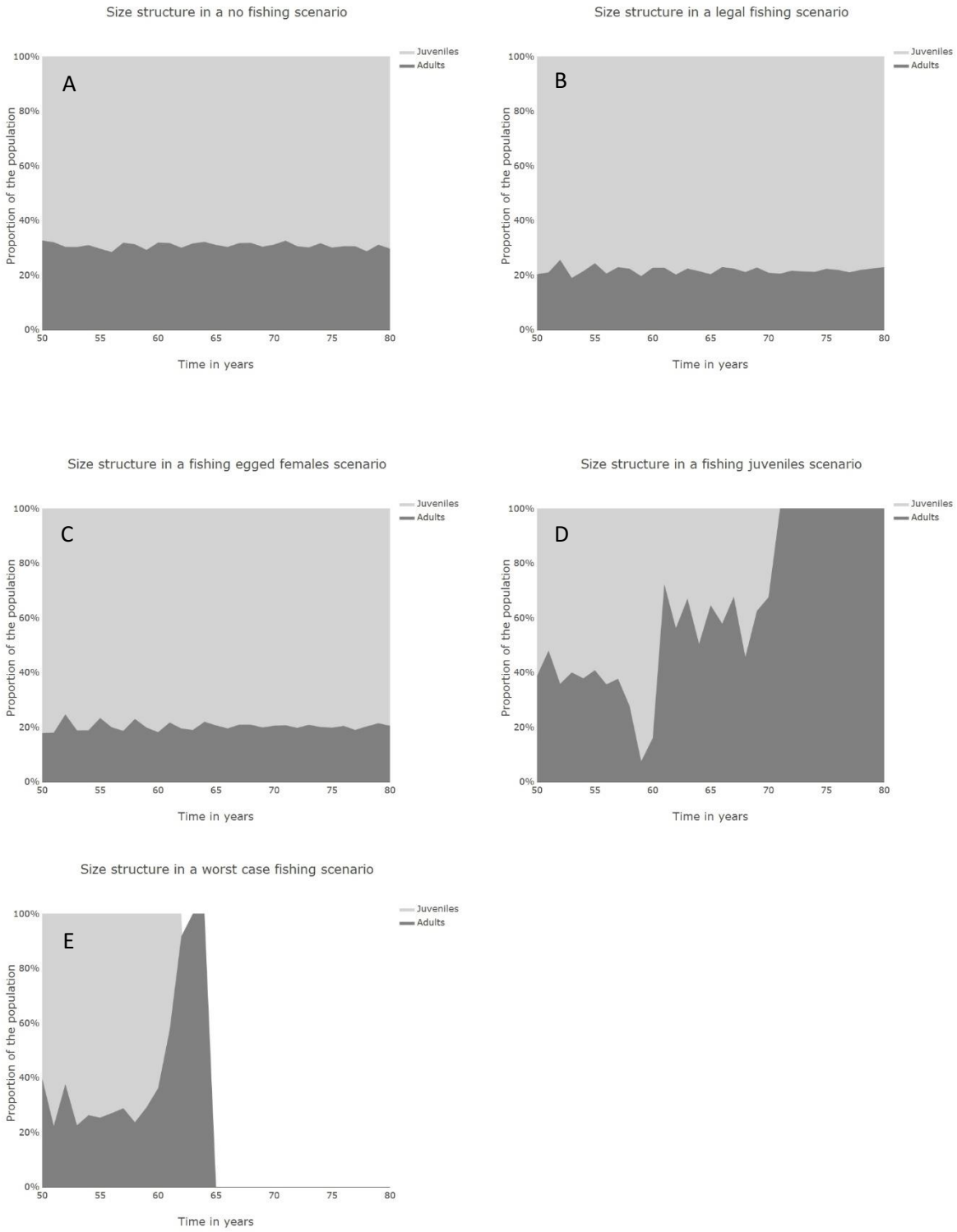


Figure 2.6. Size structure of spiny lobster population in the five scenarios simulated using the B52 model.

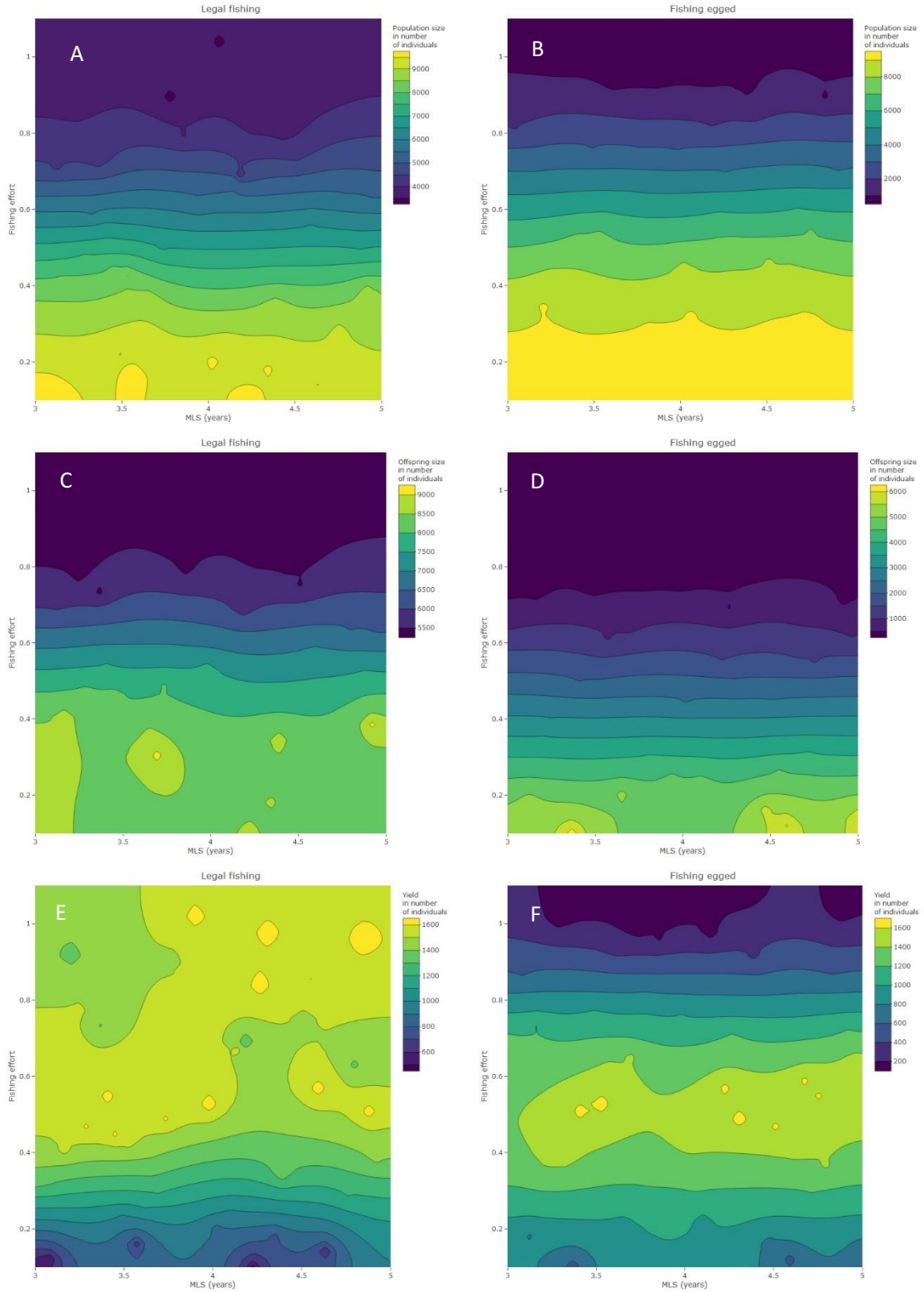


Figure 2.7. Contour plots show the global sensitivity analysis of iterating the individual based population viability analysis using the total range of values of fishing effort and MLS to reveal the strategies that maximize the population size, the production of offspring and the catch. Lighter regions indicate higher numbers.

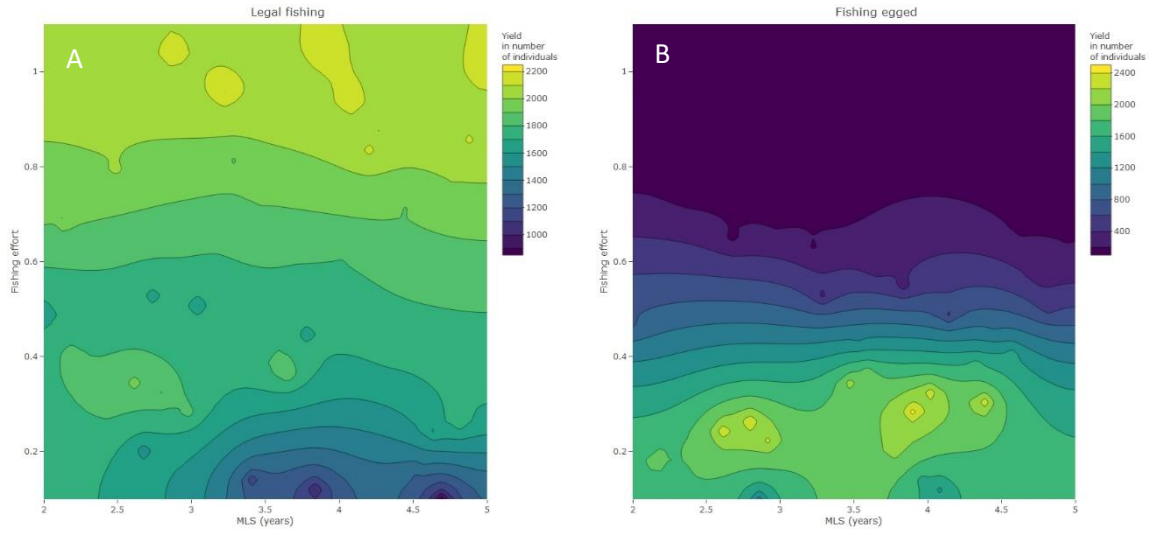


Figure 2.8. Contour plots show the global sensitivity analysis of iterating the individual based population viability analysis using an MLS smaller than the size at which individuals reach sexual maturity. Lighter regions indicate higher numbers.

2.4 DISCUSSION

In this study, the B52 Spiny Lobster model was applied to assess the effect of fisheries practices and management scenarios on the population dynamics of the green spiny lobster *P. gracilis* in the ETP. The B52 model is an individual based population viability analysis, implemented in the program Vortex 10. The modelled scenarios were 1) "legal fishing", in which a MLS and an egged female moratorium are enforced, 2) "fishing egged", with no egged female moratorium, 3) "fishing juveniles", in which no MLS is enforced, but an egged female moratorium is in place, 4) "worst case", without a moratorium and MLS, and a 5) "no fishing" scenario. The main findings of this study are that protecting juveniles and egged females as presented in the "legal fishing" scenario produce the best results in terms of catch and production of offspring. "Fishing juveniles" and a "worst case" scenarios can lead to population collapse, even with the input of offspring produced independently from the state of the adult population, and should therefore be avoided.

The population size and the production of offspring are more sensitive to variations in the fishing effort than the MLS. At low levels of fishing effort, spiny lobster population presents the highest abundance and production of offspring. However, if an egged female moratorium is in place, and no juveniles are extracted, then MLS interacts with the fishing effort showing the conditions for a maximized catch. MLS represent the size or weight at which it is optimal to extract an individual in terms of catch and to assure that the individual has contributed to the replenishment of the population. The B52 model shows that the catch is maximized at a MLS that has allowed between one to three broods per female and a medium fishing effort. Higher fishing effort will not result in additional catch, but also not in lower catch.

However, if the MLS is not accurate because of lack of research or miscalculation of the lobster body parts, then the population becomes more vulnerable to varying fishing effort. In the same way, in the absence of an egged female moratorium, MLS becomes less important and the catch is maximized only at an intermediate level. A higher and lower fishing efforts produce a smaller catch (Figure 2.7F). Management experience has proven that it is easier and less expensive to manage and control MLS

and the prohibition of catching egged females, than to control and manage fishing effort (Sundelöf et al., 2015). Therefore, directing special effort and resources to implement an accurate MLS and egged female moratorium, accompanied with an effective collaboration with the stakeholders, can be more successful than strictly controlling for some aspects of effort.

Moreover, in the case that no egged female moratorium, the production of successful offspring in the population is reduced. Furthermore, with an increased fishing effort, the remaining females are smaller and produce less successful offspring. This can lead to recruitment overfishing, which occurs when the population doesn't have enough adults to produce sufficient successful offspring. To have in place an egged female moratorium becomes even more important considering that in the last few years, worldwide researchers and managers report a declining trend in the settlement of *Puerulus*. Caputi et al. (2014) and de Lestang et al. (2015) suggest that recent declines in settlement of some lobster stocks, are caused by poor nutrition in the *Puerulus* stage. This could be due to climate change related shifts in oceanography that impact food availability. This adds to the reasons of why it is important to study and understand the effect of varying temperatures on the population dynamics of lobsters, their impacts to fisheries, and potential management strategies. Generally, increasing the spawning stock biomass is the path taken by managers to recover the population. An egged female moratorium, as well as an accurate MLS, are key to accomplish this.

The analysis of the literature revealed that values for the growth parameters, as well as SOM, and fertility functions for the same species in the region, are different among places and over time (Table 2.2). Furthermore, they are expressed taking in account different parts of the lobster body in the various studies. An accurate estimation of MLS, as well as an effective control and communication of this fishing regulation, requires a standardization of the methodology in order to make data comparable, and reveal authentic regional variability due to environmental factors such as temperature variations.

A limitation of the B52 model for its application in fisheries, is that by being implemented in Vortex 10, which as a fixed interface, it is more difficult to make direct adaptations tailored to the research or species in question. For example, in this case it was necessary to transform all size data to age. This brought two further limitations. The first one was that it was not possible to retrieve the age structure of the harvested individuals per year, in order to back calculate age to size and to weight for reporting the yield as the catch in weight. The second limitation is that considering that size increments in a year vary among individuals (Sheehy et al., 1999), localities (Briones-Fourzán & Lozano-Álvarez, 2003), and with age, it is possible to miss detail by this transformation. Furthermore, age at size relations in the ETP reported in the literature and in comparison to my calculations using empirical data, were different among each other. This turned to be important since it revealed that differences along the region, were not only present in the age at size relations, but in morphological relations of length and weight at length.

In the future, the B52 model could be further developed by learning from the implementation in Vortex 10. Ideally, a platform that allows for independent adaptations of the model should be used (for example NetLogo, Python or R). Furthermore, and as suggested by DeAngelis & Grimm (2014), modules for simulating the different life cycle events could be developed according to the availability and accessibility of spiny lobster population and fishery information. A modular design allows to link life-history events to incorporate levels of complexity. Moreover, such a model facilitates its tailoring for different species and therefore, can become broadly used.

In conclusion, this study suggests that the best management scenario is given by combining the regulations that focus on protecting juveniles, egged females and establishing a MLS that assures the reproduction of individuals before being extracted. Extracting juveniles can lead to population

collapse. An incorrect estimation of MLS could drive the population to collapse, whereas an accurate calculation will protect the population and the catch under variations of the fishing effort. However, at an accurate estimation of MLS but no egged female moratorium, the catch is only maximized at a narrow fishing effort and the risk of decline is higher.

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Annex 1.

Table A2.1. Growth parameter values for males and females of *P. gracilis* in three studies in the ETP. L_∞ is the asymptote length and refers to the total body length and CL_∞ is the asymptote given as carapace length. K represents the body growth coefficient in time ($years^{-1}$).

Study	Site	Parameter	Females	Males
Naranjo (2011)	Playa Lagarto, Costa Rica	CL_∞(mm)	121.7	166.9
		K	0.45	0.38
Reck (1983)	Galapagos Marine Reserve, Ecuador	L_∞(mm)	432	493
		K	0.33	0.315
This study	Galera San Francisco Marine Reserve, Ecuador	CL_∞(mm)	121.7	154.54
		K	0.23	0.19

Annex 2.

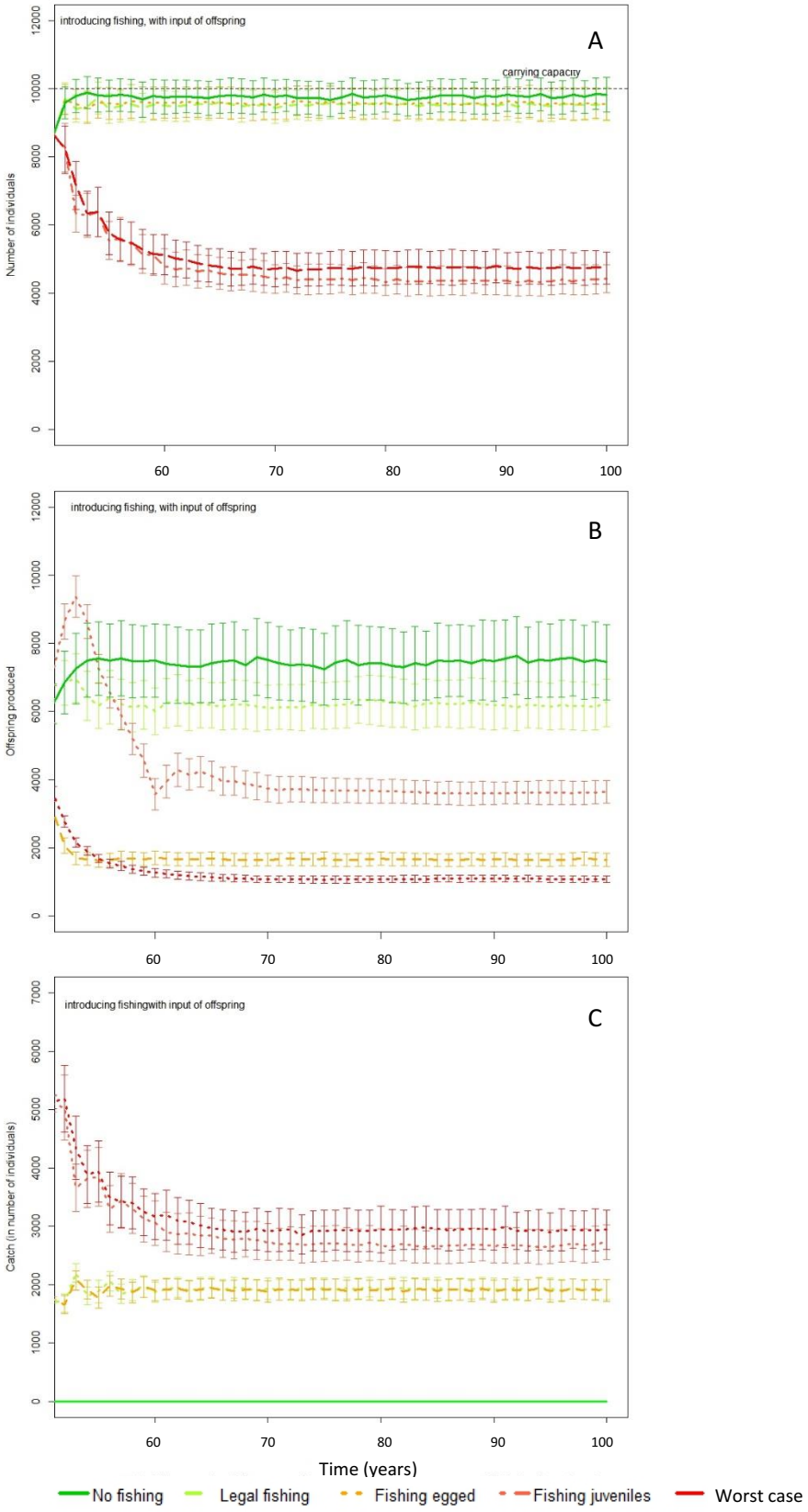

Figure A2.1. Population size (A), offspring produced (B) and catch in number of individuals (C) over time. The simulation runs for 100 years. After the first 50 years when the population has acquired a steady state, five fishing scenarios are introduced. Each of them is represented with a different color. Error bars show standard deviations for each year. Additionally to the offspring produced by the local population, external independent input is added. The assumed carrying capacity is represented by a horizontal dotted line in A. B and C are not influenced by the carrying capacity.

CHAPTER 3

Latitudinal variation of morphological relationships: a systematic review and meta-analysis of the green and red spiny lobster in the Eastern Tropical Pacific

ABSTRACT

Spiny lobsters are nowadays a delicacy and represent an important income for small scale fishermen. So much so, that in the Eastern Tropical Pacific the existing catch reports indicate that in most cases between 60% to over 90% are undersized individuals according to each country's minimum landing size (MLS) regulations. The persistence of spiny lobster populations at one locality does not exclusively depend on the local management efforts. Local recruitment is detached from local reproduction by a scattering larval phase. The prevalence of the reproductive population in oceanographically inter-connected localities is key for the perseverance of the spiny lobster populations. Therefore, a coordinated fisheries management among the inter-connected localities seems obligatory. However, no analyses have been done with a regional perspective directed to support spiny lobster fisheries management. In this study, I searched for the available literature of the green (*Panulirus gracilis*) and the red (*P. penicillatus*) spiny lobsters from the Mexico to Ecuador, including the islands that form the Tropical Eastern Pacific Marine Corridor. Only the studies showing morphological measurements of males and females were selected. I used a meta-analysis for comparing the strength of the morphological relationships represented by the correlation coefficient r^2, and a meta-regression analysis to explore the effect of geographic and environmental variables. I found that morphological relations are significantly different along the studied region. Moreover, in northern latitudes of the Eastern Tropical Pacific, where sea surface temperature (SST) is higher in average, females of both the green and red spiny lobster morphological relationships show more variability than at the Equator. None of the explanatory variables, also known as moderator variables in meta-analysis, has a statistically significant effect on males' morphological relationship strength. In terms of management, MLS regulations should be adapted accounting for the effect of sea surface temperature and its variation. Additionally, it was observed that monitoring methodologies are not standardized within the region and even in some cases, neither within countries. Furthermore, in most places monitoring of the spiny lobster fishery happens sporadically, only in Galapagos takes place every year. Identifying patterns of variations can improve the accuracy of prediction models which can help to explore, design, and apply more effective management measures, as well as promote regional coordination to support the recovery of spiny lobsters in some places and maintain them in other.

3.1 INTRODUCTION

In 2014, lobster catches worldwide marked a new record (FAO, 2016). The American lobster (*Homarus americanus*) and the Norway lobster (*Nephrops norvegicus*) account for 60% of the global lobster catches (FAO, 2017). The International Union for Conservation of Nature and Natural Resources-IUCN (2017) evaluated these two species' populations as stable. However, population status of the extracted lobster species varies around the world. The Caribbean spiny lobster (*Panulirus argus*), which follows in importance together with other *Panulirus* species in in Africa, Asia, the Americas, and Oceania (FAO, 2017), was assessed as data deficient with a decreasing trend in the population status (Butler et al., 2011). In Cuba, Mexico and the United States, despite the existing good management and control, a higher frequency and intensity of hurricanes and habitat degradation have negatively affected *P. argus* (Ehrhardt et al., 2011; Puga et al., 2013). In Nicaragua, Jamaica, the Dominican Republic, Brazil, and Colombia, the same species is reported as overexploited mainly due to considerable fisheries catches of undersized individuals (da Silva Neves et al., 2015; FAO, 2007). Most of the other exploited *Panulirus* species are classified as data deficient by the IUCN and their population trend is unknown (IUCN, 2017). In the Eastern Tropical Pacific (ETP), four *Panulirus* species are commercially exploited. *P. inflatus*, endemic to Mexico and, *P. interruptus* present along southern California and the west coast in Mexico, are assessed as least concern (Butler et al., 2011; Butler et al., 2011). *P. penicillatus* and *P. gracilis* are broadly distributed in the region. The former mostly in islands and the second one along the mainland coast and islands. Both are assessed as data deficient and an unknown and declining population trend, respectively (Butler et al., 2013; Cockcroft et al., 2011).

In this study, the focus is on the green (*P. gracilis*) and red (*P. penicillatus*) spiny lobsters in the Eastern Tropical Pacific region. Both represent an important fishery and main source of income for many small scale fishermen. Country-based studies report high percentages of juveniles in the wild catches. For instance, in Mexico, studies from different regions report between 60% to 80% (Pérez-González, 2011; Arzola-González et al., 2011; Patiño-Valencia et al., 2009), in Costa Rica 75% (Naranjo Madrigal, 2011), in Panamá 20% (Guzmán et. al, 2008) of individuals of *P. gracilis* below the countries' minimum landing size (MLS). In Mainland Ecuador, studies conducted in different years and different localities report 96% (Correa et al. 1994), 93% (Murillo Posada et al., 2013) and 98% (Figueroa & Mero, 2013 and Luna et al., this study) of undersized *P. gracilis* individuals. In Galapagos, Correa et al. (1994) reported for *P. gracilis* and *P. penicillatus* almost 52%, Bautil et al. (2003) reported 33% of undersized *P. penicillatus* and 9% *P. gracilis* for the period of 1998-1999, and Moreno et al. (2007) reported 39% for *P. penicillatus* and 15% for *P. gracilis* for the 2006 fishing season. I did not find comparable data for other countries in the Eastern Tropical Pacific Region, furthermore, in some countries there is no MLS regulation for these two species.

In order to ensure the reproduction of adult individuals before being extracted, countries' fisheries management authorities enforce a minimum landing size (MLS). MLS are informed on studies that determine the size at which a proportion of 50% of the females in a population have reproduced promoting in that way the sufficient production of eggs. This is known as the size of onset of sexual maturity (SOM). To reach sexual maturity, individuals go through a series of physiological, behavioral and morphological changes. Some of their body parts start increasing at a different range than others leading to a variation in body proportions known as relative growth (Hartnoll, 1982). Relative growth is captured in morphological linear or non-linear equations. Morphological relationships expressed as mathematical models have been used widely to estimate body part sizes from measurements of single attributes. Actual size measurements and estimations are used to report size structures, fecundity as a

function of size, and to calculate age at size. Reproductive sizes (minimum, maximum, and SOM), as well as MLS, are also expressed as measurements of lobster single attributes (e.g. carapace length or total length). Body parts that were not measured are traditionally estimated using length-length and weight-length linear or non-linear morphological relationship equations. Such size measurements and estimations feed further predictive models to calculate future yields and stock biomass levels for fisheries and population assessments (Sparre & Venema, 1998).

However, the size at which lobsters reach sexual maturity varies within species, with latitude (Hirose et al., 2012; Beyers & Goosen, 1987; Ayza et al., 2011), population density (Queirós et al., 2013), mean temperature, food availability (Annala et al.,1980; Green et al., 2014), longitude, and temperature range (Ellis et al., 2015). Temperature, for instance, affects lobster life cycle in almost all stages. The most consistent responses are in growth and reproduction (Green, et al. 2014). Growth rate is generally positively correlated to temperature within each species' thermal tolerance. Lobster species with a broad geographic distribution have certain phenotypic plasticity, meaning that they can change their behavior, morphology and physiology as a strategy to respond and adapt to environmental change. Nevertheless, when thermal tolerance maximum limits are reached, growth decreases (Hartnoll, 1982, 2001). Reproductive maturity is accelerated at higher temperatures, nevertheless, the size at SOM is also determined by population density, food availability, and other environmental and genetic variables (Ellis et al., 2015; Green et al., 2014; Queirós et al., 2013). Frequency of reproduction varies according to water temperature and latitude (Green et al., 2014). The capability of lobsters to vary phenotypic traits in response to the environment favor them to adapt to changing conditions (Green et al., 2014; Pollock, 1995), at the same time this may have a repercussion on the morphological relationships, and hence, on the population dynamics, the fisheries performance, and its management at local and regional scales.

In fact, MLS regulations vary in the region; in Mexico, MLS is 82mm carapace length (CL), in Costa Rica 80mm CL (Naranjo Madrigal, 2012), in Panamá 60mm CL or 119mm tail length (Vega et al., 2013), and in Ecuador 150mm tail length or 260mm total length (Ministerio de Comercio Exterior Industrialización y Pesca, 2001). It makes sense that MLS regulations vary, because environmental conditions that influence growth and reproduction, such as sea surface temperature (SST) and food availability, fluctuate in the ETP as well, influencing the size at which lobsters reach their sexual maturity. However, MLS have been estimated by each country independently and they are not often revised, evaluated, and adapted to the changing conditions. Furthermore, in the ETP there is no regional overview of the spiny lobster populations' dynamics and potential causes of its variability. Even more, there is no organized collaboration that takes such variations into account to establish a regional plan to recover and maintain this important fishery.

A regional awareness of the status and factors that influence the population dynamics of the green and the red spiny lobster in the ETP is particularly important, since local recruitment is detached from local reproduction by a scattering larval phase. Therefore, the persistence of spiny lobster populations at one locality does not only depend on the local management efforts. The prevalence of the reproductive population in oceanographically interconnected localities is key for the perseverance of the spiny lobster populations in a region. Therefore, a coordinated fisheries management among the interconnected localities seems obligatory. This study explores the patterns of variation of morphological relations of spiny lobsters in the ETP and potential sources based on empirical and published information available.

If we want to recover and maintain spiny lobster populations in the ETP, we need to have a better understanding on how regional environmental and geographical variables affect spiny lobster populations. Therefore, it is necessary to explore how morphological relations vary in the region to inform more accurately any MLS regulation, calculations on population dynamics, and fisheries predictive models. The approach here, is to combine all available morphological relationship equations and analyze their variability across the Eastern Tropical Pacific by means of a meta-analysis. A meta-analysis allows to use the reported statistics of the morphological relationship equations expressed as the Pearson's correlation coefficient (r^2) and make them comparable by normalizing them through a transformation to the variance-stabilizing Fisher's z. These values are further used as the effect sizes to explore the effect of sea surface temperature, Chlorophyll a concentration, absolute latitude, and longitude. To the best of my knowledge, no analyses have been done with a regional perspective directed to support spiny lobster fisheries management in the Eastern Tropical Pacific. I address the following questions:

1. How are morphological relations varying in the Eastern Tropical Pacific?
2. What are the factors that can explain such variations? Is there a clear pattern related to the moderator/explanatory variables accounted in the model?
3. Are there biases related to the model structure that are responsible for any observed variation?
    a. The combination of species?
    b. The combination of r^2 proceeding from morphological equations relating different body parts,
    c. Sampling times?

The overall motivation of this meta-analysis is to be able to compare information that otherwise wouldn't be and so, to find patterns of variability that might be important for revising and establishing MLS regulation. Furthermore, I aim to promote the importance of standardizing monitoring and reporting protocols. Only in this way, regional plans for trans-boundary protected areas, such as the Marine Corridor CMAR, can be effectively applied, evaluated and communicated.

3.2 METHODOLOGY

3.2.1 The species: the green spiny lobster (*Panulirus gracilis*) and the red spiny lobster (*Panulirus penicillatus*)

The green spiny lobster (*P. gracilis*) and the red spiny lobster (*P. penicillatus*) were selected for this study since they are the most widely distributed in the Eastern Tropical Pacific.

The green spiny lobster *Panulirus gracilis* is distributed along the coastline of the eastern Pacific, from Baja California, Mexico to Paita, Peru and the Galapagos islands. It is found in depths between 0 to 40m, among rocks, in cracks, and crevices (Briones-Fourzán & Lozano-Alvarez, 1992; Holthuis, 1991), as well as over sandy areas with gravel. It is able to tolerate a wider range of water turbidity (Briones, Lozano, Martínez-Guerrero, & Cortés, 1981; Lozano, Briones, Santarelli, & Gracia, 1982; R. Pérez-González, Flores-Campaña, & Nuñez-Pastén, 1992) than *P. penicillatus* (Olivier, 1791).

The red spiny lobster *P. penicillatus* is the most widely distributed spiny lobster in the world, extending throughout the Indo-West Pacific and the East Pacific regions (Holthuis, 1991). Chow et al. (2011) and

Abdullah et al. (2013) showed that the red spiny lobster population in the Eastern Pacific have been genetically isolated from their relatives the Central and West Pacific for ca. 1M years. In the Eastern Tropical Pacific, the red spiny lobster occurs in the Galapagos and Revillagigedo archipelagos, the Cocos and Clipperton islands (Holthuis, 1991; Holthuis & Loesch, 1967), and Malpelo island (Abele, 1975). In the mainland, it has only been reported to occur in Mexico in the regions of Sinaloa, Nayarit, and Guerrero. *P. penicillatus* is mostly found in depths from 1 to 4m and maximum 16 m, on rocky substrates, in clear waters often near the surf zone.

The life cycle of spiny lobsters, as other crustaceans is characterized by a pelagic larval stage (Figure 3.1). For *P. gracilis* and *P. penicillatus* this stage lasts for around 9 months and eleven metamorphic phases. During this time, lobster larvae also called *Phyllosoma* move with currents for hundreds or thousands of kilometers (Johnson, 1971; Johonson, 1974; Matsuda et al., 2011). In the more lobster like *Puerulus* stage, lobsters settle in small crevices at shallow coastal waters. Due to this behavior, the replenishment of local lobster populations depend on other oceanographic interconnected populations (Caley et al., 1996).

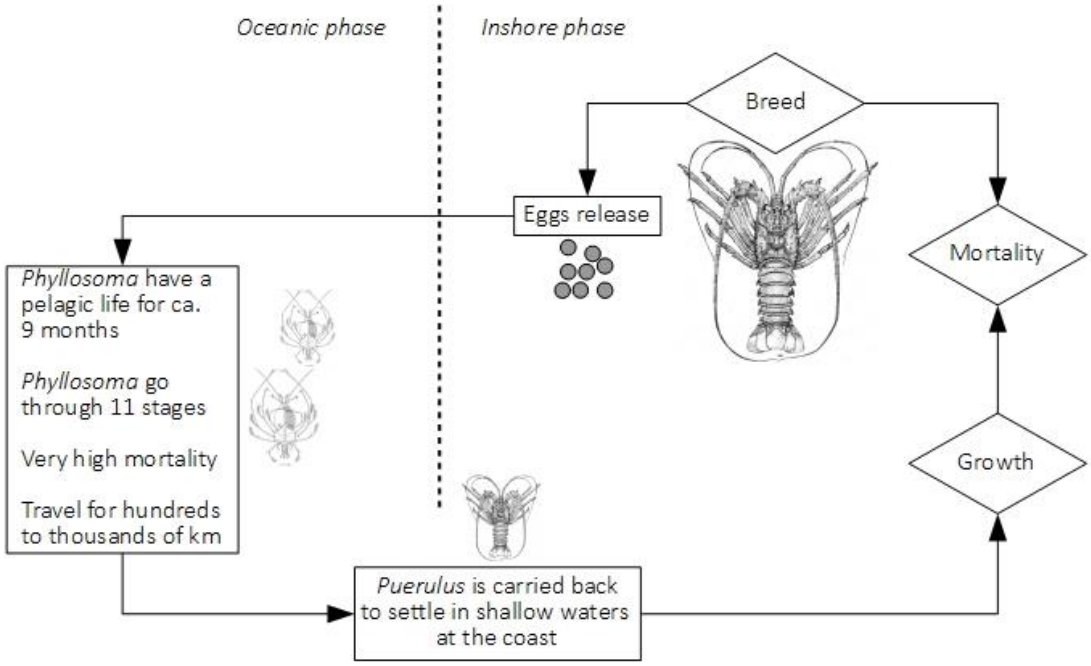

Figure 3.1. Life cycle of spiny lobsters.

3.2.2 Data sources and study selection criteria

I chose those studies that took place along the Pacific coast between Baja California and northern Peru because this is the geographical distribution of *P. gracilis. P. penicillatus* populations in this area are isolated from any other in the world (Abdullah et al., 2013; Chow et al., 2011). The next step was to select the literature that presented morphological relationships. These are commonly expressed as linear or non-linear relationship equations between two single attributes measured (i.e. carapace length CL, total length TL, tail length T, and total wet weight TW). The strength of the relationship is statistically represented by Pearson correlation coefficient r^2. Spiny lobsters show sexual dimorphism

when individuals become sexually mature. Therefore, morphological relationship equations and hence, r^2 are generally calculated for males and females separately, although some studies present pooled results. I selected all studies showing r^2 calculated for each sex separately. When no r^2 was presented but only a linear or non-linear correlation plot, I accessed them with DATA THIEF III (http://datathief.org/). With this software, I was able to reverse engineer the raw data and calculate the missing r^2.

To maintain independence of data, when studies presented two or more morphological relationships from the same data set (for example carapace length-total length and carapace length-total weight), only one relationship was selected, preferring the length-length relationship. Data from both species (*P. gracilis* and *P. penicillatus*) were analysed together in two subgroups: females and males.

For a detailed description of the literature review process see section 1.5 in Chapter 1.

3.2.3 Data analysis

I executed the meta-analysis using the package "metaphor" (Viechtbauer, 2010) in R 3.3.1 (R Core Team, 2013). I chose the normalizing and variance-stabilizing Fisher's z transform of r as the magnitude parameter i.e. the "effect size" metric for comparing, on the same scale, the common effect of interest (correlation coefficient of the morphological relationships) that was measured in the different selected studies for this meta-analysis.

$$z_r = 0.5\left[ln\frac{(1+r)}{(1-r)}\right]$$

And the variance of z_r:

$$v_{Z_r} = \frac{1}{(n-3)}$$

Where n is the sample size. Sample sizes of all studies were large enough to use this formula without inflating the variance.

First, I conducted a meta-analysis using a fixed effects model and a random effects model. The fixed effects model assumes that the estimated effect sizes of each study considered in the meta-analysis come from a single homogenous population thus, all the studies have the same true effect size. The overall effect size is the average of all studies accounting for the fact that some studies have a larger sample size (n) and therefore, are more precise. Variations are assumed to be only due to random sampling error (Koricheva et al., 2013; Schwarzer et al., 2014) thus, the fixed effects model accounts for within-study variation and not for between-study variation (τ^2). To test the assumption of homogeneity of effect sizes among the different studies in the selected region, I use the Cochran's Q-Test of heterogeneity. Cochran's Q heterogeneity test is the chi-squared statistic calculated as the weighted (w) sum of squared differences (d) between individual study effects and the overall effect across studies, with the weights being inversely proportional to the variance in each study. Therefore, Q_{total} represents the total variance. Under the null hypothesis of $\tau^2 = 0$, Q is distributed as a chi-square statistic with k (number of studies) minus 1 degrees of freedom (Higgins et al., 2003), which represents the expected variance if all studies have the same true effect (Borenstein et al., 2007):

$$Q_{total} = \sum_{i=1}^{k} w_i d_i^2 - \frac{(\sum_{i=1}^{k} w_i d_i\ )^2}{\sum_{i=1}^{k} w_i}$$

Higgins et al. (2003) and Higgins & Thompson (2002) observed that the power of this test is sensitive to the number of studies included in the meta-analysis. Furthermore, they acknowledge that there might always be some heterogeneity among studies even if these are not detected in statistical analyses. They proposed I^2as an additional index to test for inconsistency across studies. The I^2statistic expresses the percentage of variation across studies that is due to heterogeneity rather than chance and does not intrinsically depend on the number of studies considered.

$$I^2 = 100\% * \frac{Q_{total} - df}{Q_{total}},$$

where df are the degrees of freedom given by $k - 1$ (Huedo-Medina et al., 2006; Schwarzer et al., 2014). If $Q_{total} \leq (k - 1)$, then I^2 is truncated to zero to avoid a negative value. If there is very little variation between studies, then I^2 will be low, and a fixed effects model might be appropriate. Related to I^2, the between-study variance (τ^2) also serves as a measure of heterogeneity.

$$\tau^2 = \frac{Q_{total} - df}{C}$$

Where

$$C = \sum w_i - \frac{\sum w_i^2}{\sum w_i}$$

In the same way as in I^2, $Q_{total} - df$ returns the observed minus the expected variance, and C is a scaling factor that puts τ^2 in the same metric as the variance within-studies. If $Q_{total} \leq (k - 1)$, then τ^2 is truncated to zero to avoid a negative value. When the assumption of homogeneity of effect sizes doesn't apply, the heterogeneity among effect sizes of the different studies should be incorporated into a random-effects model.

The random effects model allows the study outcomes to vary in a normal distribution between studies and considers two components of variance: between studies due to random differences in their true effect size, and within studies due to sampling variance or sampling error (Koricheva et al., 2013). In this way, the variation in study-specific effects caused by different experimental conditions, locations, etc. is accounted for. The random effects model allows for different study-specific effect sizes and assumes that differences in the true effect sizes for the different studies, is due to random variation around a pooled mean effect which characterizes the population of studies (Higgins et al., 2003; Koricheva et al., 2013).

Potential bias caused by the methodological approach of comparing r^2 values derived from mixed length-length and length-weight relations, as presented in the different studies, as well as from mixing the two spiny lobster species in the analysis, was also tested and eliminated by means of a subgroup analysis. Cochran's Q-Test of heterogeneity Q_{total} can be subdivided to assist the identification of the sources of heterogeneity. When subgroups or moderator variables (explanatory variables are called moderator variables in meta-analysis) are tested, total heterogeneity Q_T is divided in Q_M and Q_E. Q_M represents the heterogeneity between groups explained by the model structure (i.e. by subgroups or the moderator variables) and Q_E is the residual heterogeneity (or heterogeneity within groups) (Higgins & Green, 2011; Viechtbauer, 2010).

Bias in a meta-analysis can also arise from small-study effects. Small-study effect refers to the phenomenon that sometimes smaller studies show different (frequently larger) effects than studies with a larger sample size (Koricheva et al., 2013; Schwarzer et al., 2014). It is generally accepted to explore for possible small-study effects in meta-analysis by using a graphical representation of the data in a funnel plot. A funnel plot shows the estimated effect sizes of each study considered in the meta-analysis against the standard error (or other measure of precision) on an inverted y-axis. If there is no small-study effect, estimated effect sizes will disperse around the common average effect. With small heterogeneity, smaller studies with a smaller sample size and thus, larger standard error will distribute farther away from the common average effect (Koricheva et al., 2013; Schwarzer et al., 2014), shaping in that way an inversed cone which gives the name to the funnel plot. Statistically, I tested for asymmetry using the regression test for funnel plot asymmetry "regtest()". This test explores if there is a correlation between the observed outcome and the selected predictor (Viechtbauer, 2010). In this case, estimates were calculated with the standard error as predictor. A significant *p-value* suggests asymmetry and its causes should be explored.

A meta-regression model was performed in order to explicitly include independent moderator continuous and categorical variables in the model to explore and explain the variability of the effect size between studies. These moderator variables (covariates, explanatory variables), as well as the effect sizes in a meta-analysis, are used in a studies-level and not in a subject-level like it would be in a single regression or in a multiple regression (Borenstein et al. , 2009). Meta-regression models diverge from simple regressions by accounting for the sample size. In that way, larger studies have more influence on the relationship than smaller ones.

I used the following meta-regression model:

$$\hat{\theta}_k = \theta + \beta_1 x_{1k} + \cdots + \beta_\rho x_{\rho k} + u_k + \sigma_k \epsilon_k, \qquad \epsilon_k \sim N(0,1);\ u_k \sim N(0, \tau^2),$$

where $k = 1, \ldots, K$, u and ϵ are independent error terms. This model is also called a mixed effects model, since it has terms from the fixed effects (β_ρ) and random effect model (u_k and variance τ^2). To describe the impact of the moderator variables, the index R^2 was used. R^2, adapted for meta-regression, indicates the true variance explained as a proportion of the total true variance. In a meta-analysis, covariates are study-level and thus they can only help to explain the between-study variance (τ^2)(Borenstein et al., 2009).

$$R^2 = 1 - \left(\frac{\tau^2_{residual}}{\tau^2_{total}} \right)$$

Furthermore, meta-regression models present the residual heterogeneity (Q_E) which is not explained by the moderator variables (Higgins & Green, 2011).

Additionally, I collected data indicating the size at which female lobsters reach sexual maturity from all available studies of the green and the red spiny lobster in the ETP region. Size at sexual maturity was presented in a number of ways. Some publications reported the average size of egged females, other the cumulative frequency at which most of the females carry eggs, and other fitted a logistic curve to the data. When possible, I accessed the data presented in tables and size frequency histograms of egged females to calculate the proportion of egged individuals in each size and to fit a logistic regression. In this manner, the size at which 50% of the females in a given population reach sexual

maturity (SOM), was estimated. The following equation where SOM is represented as CL_{50} was employed:

$$p_i = \frac{p_{max}}{(1 + e^{-a*(CL_i - CL_{50})})}$$

where p_i is the probability of carrying eggs in the i^{th} size, p_{max} is the asymptote, normally set to 1. In this case, since the only sign of sexual maturity that was noted was the carrying of eggs, p_{max} is normalized to the observed number of females carrying eggs and the number of days in the year that an individual from *P. gracilis* and *P. penicillatus* can carry eggs. a is the steepness, CL_{50} is the carapace length matching to 50% of p_{max}, and CL_i is the carapace length of the i^{th} individual. Because of the normalization of p_{max} mentioned above it was not possible to use a least-squares estimate of the non-linear model with the "nls" function in R, nor a traditional logistic function from the general linear model ("glm" function in R). Instead, I used a modified logistic link for the glm binomial family, with a link function, an inverse link function, the derivative of the inverse link function and a function that defines the number domain ("make.link" function in R) (R Core Team, 2013).

The moderator variables considered in this analysis are: latitude, longitude, mean sea surface temperature (SST), the range sea surface temperature, and Chlorophyll a concentration. Latitude and longitude were given in most studies; otherwise coordinates were assigned from the approximate center of the spatial range of sampling, as could be best deduced from the selected studies' methodologies and using Google Earth (version 7.1.5.1557). The mean sea surface temperature (SST) and Chlorophyll a concentration were extracted for each location every month during the month(s) or year(s) of the study and, if available, one previous year, since *P. gracilis* and *P. penicillatus*, molt and grow at least once per year (Briones-Fourzán & Lozano-Alvarez, 2003; Hearn & Murillo, 2008; Naranjo Madrigal, 2012). The mean SST (mean of all months in all years) and the range SST (the mean difference between the mean SST of the three coldest months in a year and the mean SST of the three warmest months of each year) were calculated for each site. SST data were extracted from the AquaModis satellite online data base and using the free software SeaDAS (Baith et al., 2001). Mean Chlorophyll a concentration of all months in all years, were calculated for each site. In this study, I considered Chlorophyll a concentration as a proxy for photosynthetic biomass production, since there is no comparable data from benthos at each site. Chlorophyll a concentration data were obtained from the SeaWifs satellite online database and using the free software SeaDAS (Baith et al., 2001). Studies that dated from before SST and Chlorophyll a concentration data availability (1994 for SST and Chlorophyll a mid-1997), were excluded from this analysis. Analyses were done for males and females separately.

3.3 RESULTS

The selection criteria were met by 14 studies which range from Piaxtla, Mexico in the north, to Ecuador (Table 3.1). Some studies present results for both species or for different localities, and therefore there are 18 cases in total. The data from the selected studies come from fisheries, scientific monitoring, or from a mixture of both. Sampling dates and time varies considerably among studies, being the earliest in 1962-1963 and the latest in 2012. In some cases, data were taken for a couple of days and in other cases, for years. The number of individuals measured in each study goes from almost 100 to over 5000. The sizes data presented come from different lobster body parts, therefore morphological relations capture in some cases the relation of carapace length-tail length (CLT), in other cases carapace length-total length (CLTL), and in other studies carapace length-total wet weight

(CLTW), and total length-total wet weight (TLTW). The meta-analysis allowed to compare the strength of the morphological relationships represented by the correlation coefficient r^2 among the selected studies grouped by sexes for both species *P. penicillatus* and *P. gracilis*.

Overall, fixed effects, as well as the random effects model of the meta-analysis, confirm that morphological relations have a strong positive effect (Figure 3.2). Estimated effect sizes show significant differences among studies in the two subgroups: males and females (see *Heterogeneity* results in Figure 3.2). The high I^2 values (in all cases close to 100%) show that most of the variability across studies is due to genuine differences underlying the results rather than by chance (sampling error). These results suggest that the random-effect model, which accounts for variation within and between studies, is more suitable for these data. A further Q-test to explore the effect of year of sampling, and of putting together the two lobster species, as well as the different length-length and length-weight relations, show to be not significant in any of the subgroups (Table 3.2), meaning that the model structure used in this study was not responsible for the heterogeneity.

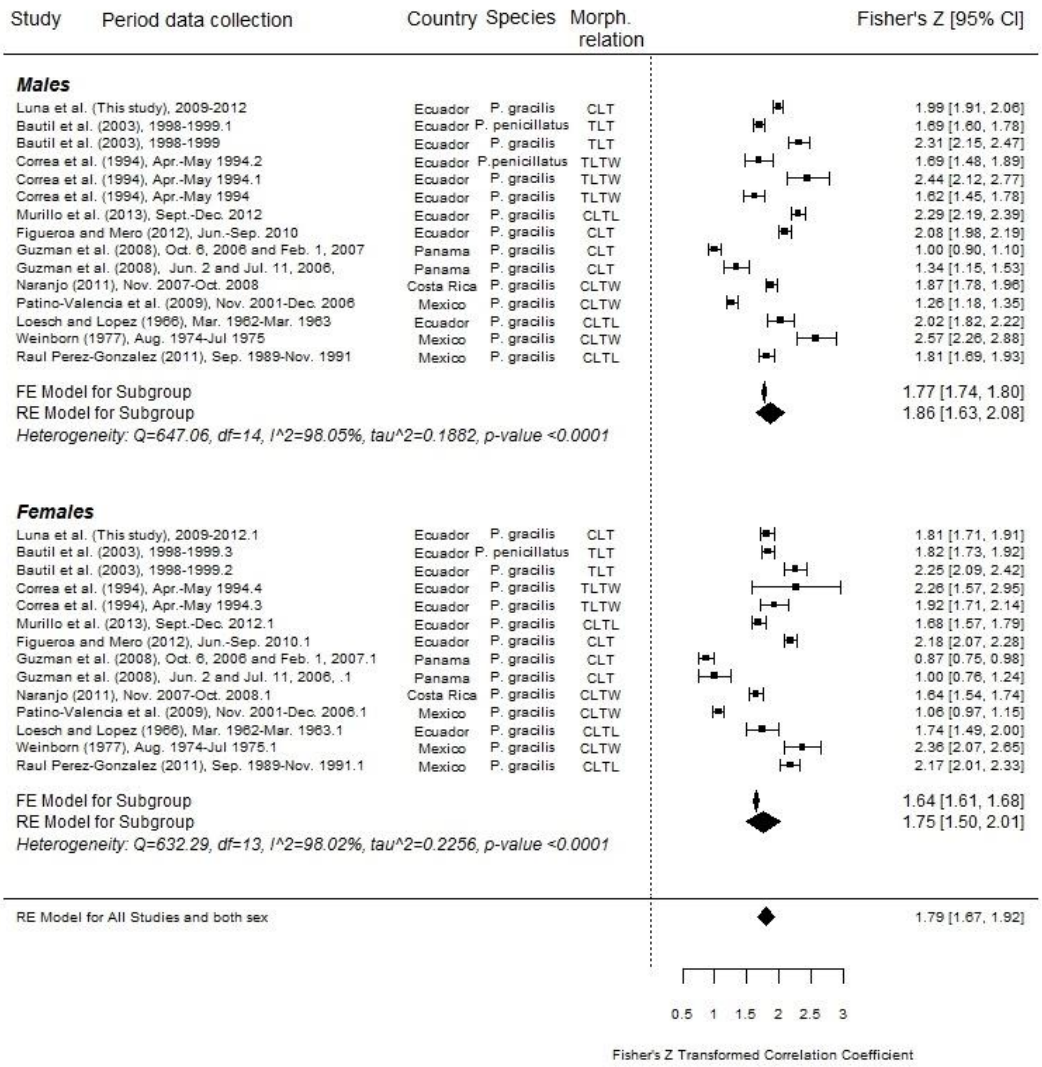

Figure 3.2. Forest plot shows the effect size for each study, for the type of morphological relationship (Morph. relation), species, country and period of data collection. It presents the average effect size of the meta-analysis using a random effects model (RE) and a fixed effects (FE) model with standard errors (95% CI). Morph. relation is built from the relative size of a combination of two of the following lobster body parts: carapace length (CL), total length (TL), tail length (T), total wet weight (TW). Heterogeneity statistics are presented for each subgroup and are given by τ^2 (estimated amount of total heterogeneity), τ (square root of estimated τ^2 value), I^2 (total heterogeneity / total variability), H^2 (total variability / sampling variability) and test of heterogeneity (Q) with corresponding degrees of freedom (df) and p–value for females and males.

Table 3.1. List of studies that met the selection criteria. Studies repeated two or more times in the list correspond to different localities or different species. The last column shows the type of morphological equation presented in each of the selected studies. These relations are built from the relative size of a combination of two of the following lobster body parts: carapace length (CL), total length (TL), tail length (T), total wet weight (TW).

Study	Sample region	Country	Sample date	Species	Latitude	Longitude	r			Sample size (n)			Type of morph. relation
							male	female	bothsex	male	female	bothsex	
Raul Perez-Gonzalez (2011)	Piaxtla	Mexico	Sep. 1989-Nov. 1991	*P. gracilis*	23,1733	-106,406	0,947629	0,974166	0,960897	271	159	430	CLTL
Weinborn (1977)	Ixtapa	Mexico	Aug. 1974-Jul 1975	*P. gracilis*	17,6229	-101,646	0,988433	0,982344	0,985389	43	50	93	CLTW
Loesch and Lopez (1966)	various sites mainland	Ecuador	Mar. 1962-Mar. 1963	*P. gracilis*	-0,6202	-80,5325	0,965401	0,940744	0,953073	96	64	160	CLTL
Patino-Valencia et al. (2009)	Sayulita	Mexico	Nov. 2001-Dec. 2006	*P. gracilis*	20,9485	-105,472	0,85235	0,785939	0,819144	526	516	1042	CLTW
CENDEPESCA (2012)	Playas Negras	El Salvador	Feb.-Oct. 2011 and Jan. - May 2012	*P. gracilis*	13,15806	-87,9369	NA	NA	0,898777	NA	NA	1659	CLTW
Naranjo (2011)	Playa Lagarto	Costa Rica	Nov. 2007-Oct. 2008	*P. gracilis*	10,1182	-85,8534	0,953939	0,927362	0,940651	486	357	843	CLTW
Guzman et al. (2008)	Las Perlas	Panama	Jun. 2 and Jul. 11, 2006	*P. gracilis*	8,4571	-78,8841	0,87178	0,761577	0,816679	108	69	177	CLT
Guzman et al. (2008)	Coiba	Panama	Oct. 6, 2006 and Feb. 1, 2007	*P. gracilis*	7,4632	-81,9585	0,761577	0,7	0,730789	382	297	679	CLT
Arzola-Gonzalez et al. (2011)	Sinaloa	Mexico	1995-1997	*P. gracilis*	23,48361	-106,668	NA	NA	0,886961	NA	NA	5062	CLTL
Figueroa and Mero (2012)	El Mangle-Puerto Cayo and Puerto Lopez-Salango	Ecuador	Jun.-Sep. 2010	*P. gracilis*	-1,3718	-80,8691	0,969536	0,974679	0,972108	352	351	703	CLT
Murillo et al. (2013)	Anconcito	Ecuador	Sept.-Dec. 2012	*P. gracilis*	-2,33755	-80,8972	0,979796	0,932738	0,956267	370	337	707	CLTL
Correa et al. (1994)	various sites mainland	Ecuador	Apr.-May 1994	*P. gracilis*	-0,92	-90,85	0,924338	0,958228	0,941283	147	89	236	TLTW
Correa et al. (1994)	various sites Galapagos	Ecuador	Apr.-May 1994	*P. gracilis*	2,4341	-80,7715	0,984987	0,978468	0,981728	39	11	50	TLTW
Correa et al. (1994)	various sites Galapagos	Ecuador	Apr.-May 1994	*P.penicillatus*	-0,6731	-90,1597	0,933542	NA	NA	92	51	143	TLTW
Hearn (2005)	various sites Galapagos	Ecuador	2000-2005	*P. penicillatus*	-0,8274	-89,6305	NA	NA	0,964261	208	275	483	TLTW
Bautil et al. (2003)	various sites Galapagos	Ecuador	1998-1999	*P. gracilis*	-1,0909	-91,0909	0,980408	0,978059	0,979234	151	144	295	TLT
Bautil et al. (2003)	Galapagos	Ecuador	1998-1999	*P. penicillatus*	-0,84	-89,3282	0,934452	0,94921	0,941831	470	422	892	TLT
Luna et al. (This study)	San Francisco Cape	Ecuador	2009-2012	*P. gracilis*	0,8622	-80,0598	0,9632	0,9481	0,95565	666	371	1037	CLT

Table 3.2. Heterogeneity explained by the model structure, corresponding degrees of freedom, and p-value to test the effect of the methodological approach of analysing together the two spiny lobster species and the different morphological relationships.

	Q_M	df	$p-value$
Effect species (factorial variables)			
Males	0.3206	1	0.5713
Females	0.0203	1	0.8867
Effect of type of morphological relations (factorial variables)			
Males	1.7271	4	0.7858
Females	2.6691	4	0.6146
Effect of year (continuous variables)			
Males	1.1914	1	0.2750
Females	1.6679	1	0.1965

The funnel plot, which allows to visualize possible small-study effects, show how less precise studies fall outside the confidence interval (95%). The regression test for funnel plot asymmetry regtest(), confirms that in the subgroup "males" (z = 1.9132, p-value = 0.0557) exists small-study effects. I removed from the data set the studies causing the effect which were the ones with a sample size smaller than 100. This returned a non-significant p-value of the newly run regtest().

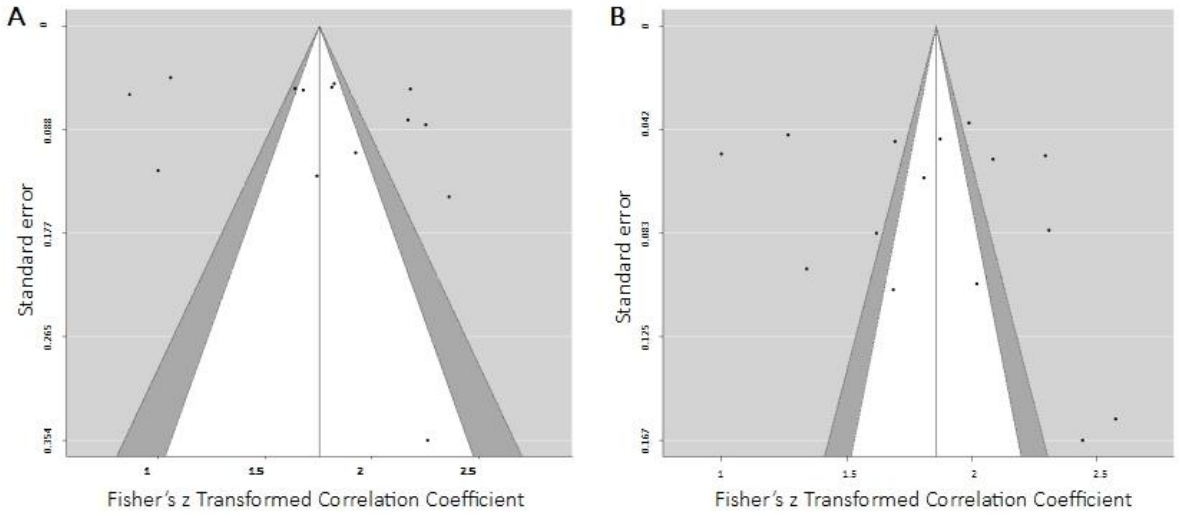

Figure 3.3. Funnel plot to explore asymmetry of the distribution of estimated effect sizes around the average effect for A. females and B. males. White area of the funnel represents 99% CI and dark grey area the 95%CI.

The meta-regression test shows that in all subgroups the residual heterogeneity decreases when considering moderator variables to explore their effect on the variation of the morphological relationship strength (see Q values for each subgroup in Table 3.3). Latitude was removed from the model to avoid collinearity with mean SST.

Table 3.3. Estimated effect sizes (Zr) calculated with a random effects model and the corresponding standard error (se), Z values and p – values to assess the effect of mean and the range of sea surface temperature (SST), the mean concentration of chlorophyll a, and longitude on the strength of the morphological relationship for spiny lobster A. females and B. males. Latitude was removed from the model to avoid collinearity with mean SST.

A. Females			
Random effects model without moderator variables:			
	Effect size (se)	*Z value*	*p – value*
Intercept	1.7546 (0.1305)	13.4406	<.0001
AIC 22.2954 τ^2 (estimated amount of total heterogeneity): 0.2256 (SE = 0.0933) I^2 (total heterogeneity / total variability): 98.02% H^2 (total variability / sampling variability): 50.57 Test for Heterogeneity: Q (df = 13) = 632.2994, p-value < .0001			
Random effects model with moderator variables:			
Moderators	*Effect size (se)*	*Z value*	*p – value*
Intercept	11.9294 (2.3676)	5.0387	<.0001
Mean SST	-0.5388 (0.1437)	-3.7481	0.0002
Range SST	-0.2182 (0.0988)	-2.2085	0.0272
Mean Chlorophyll a concentration	-0.8137 (0.3820)	-2.1300	0.0332
Longitude	0.0698 (0.0320)	2.1818	0.0291
AIC 12.2955 τ^2 (estimated amount of residual heterogeneity): 0.0599 (SE = 0.0456) I^2 (residual heterogeneity / unaccounted variability): 93.92% H^2 (unaccounted variability / sampling variability): 16.45 R^2 (amount of heterogeneity accounted for): 75.96% Q_E (df = 4) = 81.1091, p-value < .0001 Q_M (df = 4) = 27.3886, p-value < .0001			
Random effects model with one moderator variable:			
Intercept	7.9744 (1.5305)	5.2102	<.0001
Mean SST	-0.2370(0.0568)	-4.1761	<.0001
AIC 8.3714 τ^2 (estimated amount of residual heterogeneity): 0.0784 (SE = 0.0442) I^2 (residual heterogeneity / unaccounted variability): 95.94% H^2 (unaccounted variability / sampling variability): 24.62 R^2 (amount of heterogeneity accounted for): 68.54% Q_E (df = 7) = 173.4304, p-value < .0001 Q_M (df = 1) = 17.4398, p-value < .0001			
Comparison of models with moderator variables *versus* the null model			
Model without moderator variables: τ^2 total = 0.2256 (SE = 0.0933), Q_E= 632.2994, df = 13, p-value < .0001			
Model with all moderator variables: τ^2 total = 0.0599 (SE = 0.0456), Q_E= 81.1091, df = 4, p-value < .0001 Proportion of total between-study variance explained by the model R^2 analog = 1-(0.0599/0.2256) *100 = 73.4%			
Model with moderator variable mean SST: τ^2 total = 0.0784 (SE = 0.0442), Q_E= 173.4304, df = 7, p-value < .0001 Proportion of total between-study variance explained by the model R^2 analog = 1-(0.0784 /0.2256) *100 = 65.2%			

B. Males			
Random effects model without moderator variables:			
	Effect size (se)	*Z value*	*p – value*
Intercept	1.8574 (0.1142)	16.2595	<.0001
AIC 21.0734 τ^2 (estimated amount of total heterogeneity): 0.1882 (SE = 0.0739) I^2 (total heterogeneity / total variability): 98.05% H^2 (total variability / sampling variability): 51.31 Test for Heterogeneity: Q (df = 14) = 647.0680, p-value < .0001			
Random effects model with moderator variables:			
Intercept	8.8992 (3.1760)	2.8020	0.0051
Mean SST	-0.3033 (0.1916)	-1.5827	0.1135
Range SST	-0.0750 (0.1325)	-0.5657	0.5716
Mean Chlorophyll a concentration	-0.1088 (0.5129)	-0.2122	0.8320
Longitude	0.0174 (0.0427)	0.4073	0.6838
AIC 14.6865 τ^2 (estimated amount of residual heterogeneity): 0.1116 (SE = 0.0814) I^2 (residual heterogeneity / unaccounted variability): 97.48% H^2 (unaccounted variability / sampling variability): 39.65 R^2 (amount of heterogeneity accounted for): 48.23% Q_E (df = 4) = 166.0132, p-value < .0001 Q_M (df = 4) = 11.2460, p-value = 0.0239,			
Random effects model with one moderator variable:			
Intercept	7.5754 (1.5032)	5.0396	<.0001
Mean SST	-0.2159 (0.0557)	-3.8757	0.0001
AIC 8.0797 τ^2 (estimated amount of residual heterogeneity): 0.0763 (SE = 0.0426) I^2 (residual heterogeneity / unaccounted variability): 96.63% H^2 (unaccounted variability / sampling variability): 29.63 R^2 (amount of heterogeneity accounted for): 64.60% Q_E (df = 7) = 237.4094, p-value < .0001 Q_M (df = 1) = 15.0212, p-value = 0.0001			
Comparison of models with moderator variables *versus* the null model			
Model without moderator variables: τ^2 total = 0.1882 (SE = 0.0739), Q_E = 647.0680, df = 14, p-value < .0001			
Model with all moderator variables: τ^2 total = 0.1116 (SE = 0.0814), Q_E = 166.0132, df = 4, p-value < .0001 Proportion of total between-study variance explained by the model R^2 analog = 1-(0.1116 /0.1882) *100 = 40.7%			
Model with moderator variable mean SST: τ^2 total = 0.0763 (SE = 0.0426), Q_E = 237.4094, df = 7, p-value < .0001 Proportion of total between-study variance explained by the model R^2 analog = 1-(0.0763 /0.1882) *100 = 59.5%			

The females' variation of the morphological relationship strength is best explained by the meta-regression model which includes the four moderator variables: longitude, mean SST, range SST and mean Chlorophyll a concentration. In this case, all variables are significant, with mean SST as the most significant. A test with only mean SST as the moderator variable, shows an increase in the residual heterogeneity (Table 3.3A) and a higher AIC. When excluding mean SST from the meta-regression model, the test for moderators (Q_M) is not significant.

In the case of the males, the model including all moderator variables returns a significant Q_M, but none of the moderator variables appear to have a significant effect (Table 3.3B). However, when testing only mean SST, it is highly significant, the test for moderators is stronger, τ^2 and AIC decreases, but the residual heterogeneity increases from 166.0132 with 4 df to 237.4094 with 7 df.

Furthermore, the relationship between effect size and mean SST shows that in all cases morphological relationships are strong, but seem to be stronger at lower temperatures at the Equator. The strength

of this relationship decreases gradually towards higher temperatures (Figure 3.4). Since, in this region, mean SST and latitude are positively correlated, mean lower sea surface temperatures at the Equator presented a stronger relationship than at higher latitudes (Figure 3.4).

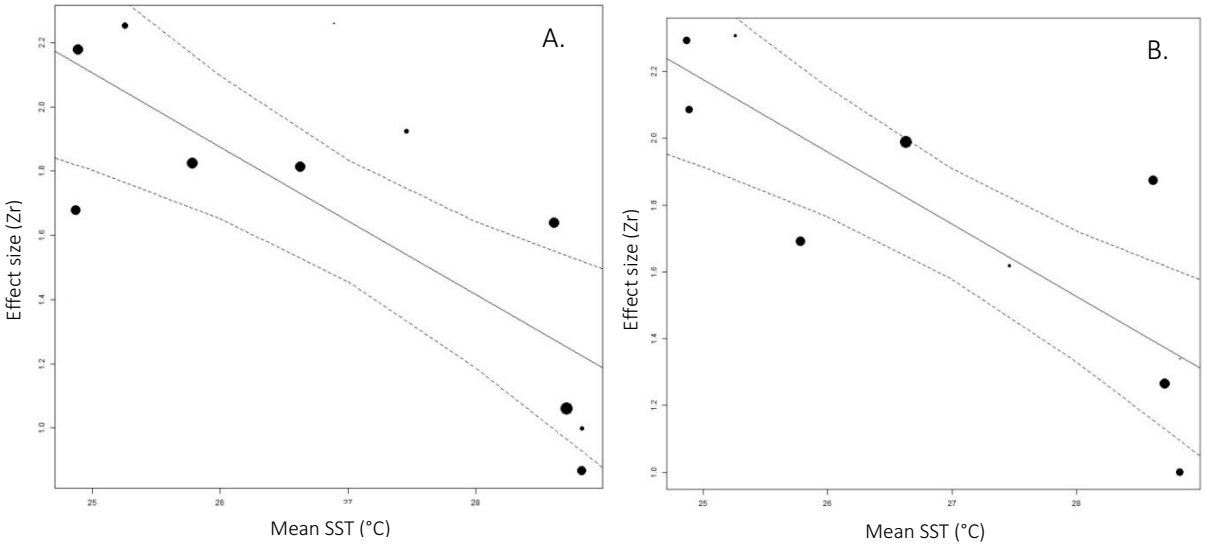

Figure 3.4. Relationship between the effect size (Zr) of the morphological relationships and mean sea surface temperature (SST). Effect sizes are showed as Fisher's Z values. Lines show the fitted regression and the 95% confidence interval. Relationships are shown for A. females and B. males. The point size represents the weight of the study and it's given by the inverse of the variance of the effect size.

Adjusted SOM values in the region varied (Table 3.4). The multiple regression to explore the effect of environmental and geographic variables on the size at sexual maturity showed no significant influence of any of the predictor variables (Table 3.5). However, SOM values showed to be positively related to minimum sizes of egged females (Figure 3.5). The smaller the egged females, the smaller the SOM.

Table 3.4. Available size of onset of sexual maturity (SOM) from different studies in the ETP taken at various years. SOM is given as the carapace length in mm.

Study	Site	Year sampled	Number of females sampled	SOM (CLmm)
Briones and Lozano (1977)	Ziguantanejo, Mexico	1976-1977	-	75
Briones and Lozano (1992)	Ixtapa, Mexico	1979-1980	-	75
Briones (2014)	Ziguantanejo, Mexico			
Perez-Gonzalez et al. (2012)	Sinaloa, Mexico		259	
CENDEPESCA (2012)	Playas Negras, El Salvador	2011-2012	-	54
Naranjo (2012)	Playa Lagarto, Costa Rica	2007-2008	357	75
Guzman et al. (2008)	Las Perlas, Panama	2006	69	84
Guzman et al. (2008)	Coiba, Panama	2007	297	84
Toral et al. (2002)	various sites Galapagos, Ecuador	1998-2000	8	88
Loesch and Lopez (1966)	various sites mainland, Ecuador	1962-1963	64	89,5
Mero et al. (2015)	Santa Rosa, Ecuador	2012	273	83
Murillo et al. (2013)	Anconcito, Ecuador	2013	337	80
This study	Galera San Francisco Marine Reserve, Ecuador	2012	371	60

Table 3.5. Multiple linear regression results showing the impact of each variable on the size at sexual maturity (SOM) variation.

	$\beta\ (SE)$	$p-value$
Intercept	127.9509 (128.2046)	0.375
Longitude	-0.4529 (1.2589)	0.737
range SST °C	-1.9287 (2.6581)	0.508
mean SST °C	-1.7353 (2.5327)	0.531
mean Chl a	-0.9597 (2.3540)	0.704
Min Size mm CL	0.8481 (0.6054)	0.234
Multiple R-squared: 0.6555, Adjusted R-squared: 0.2248 F-statistic: 1.522 on 5 and 4 DF, p-value: 0.3525		

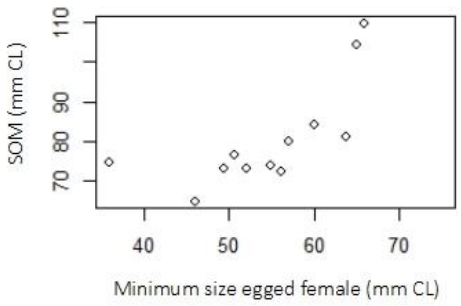

Figure 3.5. Scatterplot showing the relationship between size at onset sexual maturity and minimum size at sexual maturity expressed as the egged females.

3.4 DISCUSSION

In this research, a meta-analysis allowed me to compare various scientific studies conducted in the ETP, investigating spiny lobster morphological relations such as length-length and length-weight. A meta-regression analysis, as part of the meta-analysis, was used to investigate the patterns and the potential causes of heterogeneity among studies. The most important result is that spiny lobster morphological relations exhibit a regional pattern in the ETP. This pattern can be explained by sea surface temperature variation. Morphological relationships of lobsters measured in localities at northern latitudes, show larger variability than the relationships of lobsters measured at the Equator. In the ETP, the sites at the Equator, hold lower mean annual sea surface temperatures than localities at the north. A number of studies demonstrate that temperature play a major factor influencing the rate of metabolism and amount of growth, food availability, timing of molting, mating, spawning, and recruitment (see for example Beyers & Goosen, 1987; M. J. Butler et al., 2009; Chubb, 2000; Raúl Pérez-González et al., 2012; Putten et al., 2015; Quinn & Rochette, 2015; Serfling & Ford, 1975). This study shows that temperature also plays an important role in spiny lobster morphological relationship (length-length and length-weight) variability and therefore, can be added to this list of properties influenced by temperature. It is to expect that variations in temperature may alter these properties consequently having cascading effects on the population dynamics.

The literature reviewed in this study showed two types of differences in the information presented regarding sexual maturity. The first issue that was observed is that size at sexual maturity is presented in various ways. Some publications reported the average size of egged females, other the cumulative frequency at which most of the females carry eggs, and other fitted a logistic curve to the data showing egged females at the different size classes. This limitation was solved, when possible, by accessing the data presented in tables and size frequency histograms of egged females to calculate the proportion of egged individuals in each size and to fit a logistic regression. In this manner, the estimated size at which 50% of the females in a given population reach sexual maturity (SOM) was comparable among studies.

The second type of difference observed in this study is that the adjusted SOM values in the region showed further variations (Table 3.4). MacDiarmid & Sainte-Marie (2006) and Queirós et al. (2013) suggest that variations of the size of onset maturity might be due to local environmental conditions,

population density, and exploitation regimes. Thus, MLS regulations need to consider SOM variations among areas. Since SOM is used to inform MLS, I expected that SOM would follow similar regional patterns of variation as was shown for MLS. Contrary to this expectation, this study shows that SOM had no significant influence from any of the environmental and geographic variables tested, not even temperature as was expected. Green et al. (2014) and MacDiarmid & Sainte-Marie (2006) state that at higher temperatures spiny lobsters reach sexual maturity earlier and are generally smaller in size than lobsters in temperate waters. Spiny lobsters starting reproduction earlier will have less energy available for growth than those that reproduce later. This would suggest that minimum sizes of sexual maturity and SOM are smaller in the studies that sampled localities with a warmer mean annual temperature. This is however not the case. The variation of minimum size of sexual maturity and SOM along the region can't be explained only by temperature and other factors such as food availability, or density must have an effect. Nevertheless, SOM showed a direct positive relation to the minimum size of sexual maturity. This is particularly important for managers to consider when taking decisions around decreasing MLS to match SOM in order to attain the highest productivity of the population.

Identifying patterns at a regional scale and exploring the factors responsible of those patterns inform management at a broader scale. Spiny lobster populations are interdependent of each other in the region through their larval stage. Understanding how environmental conditions affect adult reproductive populations in the interconnected localities aids to improve fisheries assessments and to identify appropriate management for each region. Furthermore, the results presented in this study may be added as criteria to identify more resistant areas where management should focus to assure the flux of larvae are maintained.

In this study, the meta-analysis allowed me to combine and analyse information that otherwise would not have been possible. The independent studies selected through the literature review presented different morphological relations of length and weight at length. The meta-analysis allowed to generalize results to a larger "population of studies" by combining the individual studies through the use of a normalized effect size. In this study the effect size represented the correlation coefficient of the morphological relationships (r, transformed to the normalizing and variance-stabilizing Fisher's z). Additionally, the meta-analysis allowed me to investigate publication bias and to identify and explain inconsistencies between studies. Finally, with this method I was also able to explore the source of the heterogeneity among studies, which is one of the main uses of meta-analysis in ecology. In this way, this study unraveled a before unknown piece of information which can be relevant for a regional coordinated management of lobsters if the aim is to recover and maintain the populations and fisheries.

A common criticism to meta-analysis is about their validity when combining heterogeneous studies (see for example Markow & Clarke, 1997; Koricheva et al., 2013). This limitation was overpowered by exploring the possible sources of heterogeneity. I learned that most of the variability across studies is due to genuine differences underlying the results rather than by chance (sampling error). The Q-test of heterogeneity, part of the meta-analysis, permitted to test if the structure of the data caused any effect on the results. The effect of year of sampling, combining two lobster species that share habitat in the ETP, as well as combining the different length-length and length-weight relations were not responsible for the observed heterogeneity. Through this method, it was possible to identify and eliminate the studies that showed publication bias. Finally the meta-analysis allowed to test and identify the environmental and geographic factors, also called moderator variables, responsible for the variation between studies. Furthermore, the meta-regression added to the analysis by showing the form of the relation at the regional level.

The combined analysis of regional data reveals the patterns of variation of spiny lobster morphological relationships related to environmental and geographic factors. Relations between relative body measures, such as length to length and length to weight, are more variable at northern latitudes in the ETP, where the mean annual sea surface temperatures are higher than at lower temperatures at the Equator. Since reproduction and the amount and quality of eggs are related to a lobster individual size, the found variability may affect stock and population assessments as well as accurate estimations of a minimum landing size. The sizes at which 50% of the females in the population has reached sexual maturity (SOM) didn't show any effect of latitude, longitude, Chlorophyll a concentration, or sea surface temperature, but it was positively related to the size at first maturity. Studies have proven that decapod populations under pressure start reproducing earlier in their life in order to compensate the peril. Adaptations of fisheries management measures such as minimum landing size, should consider this finding before decreasing it since it would worsen the pressure over the exploited population. As a result, the data presented here provide a basis to designing the regional management of the green spiny lobster by incorporating the effects of relative sizes variability related to temperature and the sizes at maturity to inform fisheries analysis and population estimations, considering as well climate change and the high market demand.

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CHAPTER 4

Morphological relation variations and implications for Minimum Landing Size regulations for the green spiny lobster (*Panulirus gracilis*) in Ecuador

ABSTRACT

Minimum landing size (MLS) is a broadly used and accepted management regulation. Sizes subject to regulation are directly measured or calculated using equations which describe the relation between lengths of two body parts. These length-length relations allow the incorporation of empirical data into the regular statistics for stock assessment, management, and fisheries regulations. In Ecuador small scale fishermen catch high percentages of undersized green spiny lobster, suggesting management is not appropriate or regulations are not enforced. I compared length-length relations found in different lobster studies conducted along the coast of mainland Ecuador and Galapagos to explore spatial and temporal variations and possible causes. I hypothesized that water temperature is the main site-specific environmental variable driving morphological variations. Linear relations' slopes and possible causes of variation were examined using linear and multiple regression models. I found length measurements were taken in different ways: some studies included the plate between the lobsters' eyes and antenna and others did not. Therefore, I conducted a unification of the different measuring methods using size conversion factors. These standardized length-length relations were significantly different among sexes, in time and by all sites. Most importantly, I show that current minimum size regulations are not applicable to all sites. I also found that time and site specific water temperature has a significant effect on morphological relationship variations. However, it was not the main site-specific variable responsible for explaining such variations. In general, this work emphasizes the need for length data collection standardization and the consideration of temporal and spatial variation implications in national and regional fishery management planning, enforcement and evaluation.

4.1 INTRODUCTION

Minimum landing size (MLS) is the most applied regulation for lobster fisheries worldwide. They assure that individuals reproduce before being exploited. Most commonly, lobster MLS are based on the carapace length. However, lobsters are traded in tails or whole for national and international markets. When lobsters are presented as tails, carapace or total length is calculated using length-length linear relation equations. Such equations are accepted and used as standard models to calculate the missing size based on the existing data, assuming relative sizes maintain a constant ratio. In this way, morphological relationships (such as the length-length linear relation) use the empirical field data to produce the standard statistics for stock assessment, management and fishery regulations. The MLS regulation in Ecuador is 260 mm total length or 150 mm tail length (Ministry Agreement No.182, 2001). This is applied for two species: the red spiny lobster (*Panulirus penicillatus*), abundant only in the Galapagos Islands, and the green spiny lobster (*Panulirus gracilis*) present in both, the Galapagos Islands and the mainland coast of Ecuador. Despite fisheries regulations, *P. gracilis* mean capture sizes have declined in the mainland (Figure 4.1). Furthermore, fisheries catches along the mainland coast present over 90 % of undersized lobsters (Correa et al., 1994; Figueroa & Mero, 2013; Murillo Posada et al., 2013; Villón et al., 2000). In Galapagos, mean capture sizes varied in time, but were not lower than the MLS (Figure 4.1). This information shows that mainland lobster populations deteriorated in time and that regulations were not implemented or are not appropriate. On the other hand, the same regulations seem to be working for Galapagos. In this study, I compare the existing length-length linear relationships in studies in the mainland and Galapagos, explore their patterns of spatial and temporal variation and potential causes using linear and multiple regression models.

Lobsters are able to react quickly to changes in temperature and food availability. Temporal and spatial varying conditions may affect lobster population dynamics, growth rates and relative growth, influencing also fisheries performance. Such variations are important to consider in order to design appropriated management regulations, among them MLS.

Previous studies show that length-length relation equations can capture the relative growth of lobsters. Spiny lobsters adjust their relative growth in response to changing environmental conditions (Pollock, 1995). Growth rates and body sizes, of these ectothermic organisms, depend strongly on temperature (Whitman & Agrawal, 2009) as is common also for other Decapods. In order to increase their size, lobsters molt by discarding their hard exoskeleton and by hardening a new one on the soft body. Higher temperatures shorten intermoult period and increase moult increment (Serfling & Ford, 1975; Briones-Fourzán & Lozano-Álvarez, 2003; Gracía & Kensler, 1980; Green et al., 2014; Newman & Pollock, 1974). Variations in food availability can be driven by temperature amongst other factors and influences growth rates as observed by Newman & Pollock (1974) and Pollock (1986). Furthermore, higher temperature and increased food availability accelerate the ovarian development and reproductive maturity (Annala, et al., 1980). As a general rule, lobsters grow faster and reproduce more often in warmer waters than in temperate regions, and individuals grow larger where food supply is adequate and abundant (Briones-Fourzán & Lozano-Álvarez, 2003; Green et al., 2014; Pollock, 1986).

A further source of variation in morphological length-length relationships in *P. gracilis* is given by sexual allometry, meaning that the proportions of the carapace or the tail size towards the total body size differ in females and males with sexual maturity. Generally, sexually mature females develop longer and heavier tails than males of the same size (Loesch & Lopez, 1966; Figueroa & Mero, 2013; Hearn, 2005; Murillo Posada et al., 2013; Naranjo Madrigal, 2011). For this reason, equations that

describe morphological relations such as length-length are more precise if they are expressed for males and females separately. Furthermore, morphological variations have also been described in space and time. Briones-Fourzán & Lozano-Álvarez (2003) report that the green spiny lobster (*P. gracilis*) has significant differences of growth increments among sexes and seasons in two sites separated by only a couple of kilometers from each other in Guerrero, Mexico. In addition, Newman & Pollock (1974) describe how growth increments of the male rock lobster *Jasus lalandii* in South Africa varied significantly among years.

In this context, this study contrasts current MLS regulation to lobster morphological variations in time and space, considering sexual dimorphism. In this study, I extract the before mentioned aspects of size variation and analyse the relative growth of body parts in relation to time and space. Possible patterns and drivers of variation in order to recognize potential pitfalls for management enforcement were explored. The specific questions are: 1. How does the length-length relationship vary among sites and in time? 2. How relevant are these variations considering the current MLS regulation? 3. Is water temperature the environmental factor with most influence on lobster morphological variations?

I explore these questions by comparing the existing linear relations presented in all studies carried out at different times and localities in Galapagos and along the mainland coast. I use linear and multiple regression models to infer at this scale the potential drivers of morphological relations in Ecuador, as a case example.

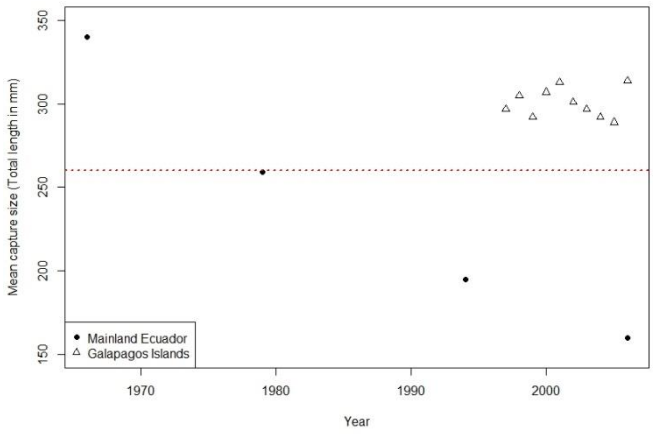

Figure 4.1. Green spiny lobster (*P. gracilis*) mean landing sizes for mainland Ecuador and the Galapagos Marine Reserve, reported by Correa et al. (1994); Cún & Campos (1993); Delhaye & Ormaza (2006); Hearn (2005); Loesch & Lopez (1966); Toral et al. (2002). The red line shows the minimum landing size (MLS) of 260 mm total length.

4.2 METHODS

4.2.1 The species: green spiny lobster (*Panulirus gracilis*)

P. gracilis geographic distribution is restricted to the eastern Pacific, from Baja California, Mexico to Paita in Peru, and the Galapagos islands. It inhabits coasts with water depths between 0 to 40m, among rocks, in cracks and crevices (Briones-Fourzán & Lozano-Alvarez, 1992; Holthuis, 1991; Holthuis & Loesch, 1967). It is also found over sandy areas with gravel since it tolerates a wide range of water turbidity (Briones et al., 1981; Lozano et al., 1982; Pérez-González et al., 1992). The life cycle of the green spiny lobster is characterized by a long pelagic larval stage. Larvae travel for around nine months while it metamorphoses before settling in small crevices at shallow coasts. Therefore, the

local recruitment has little or nothing to do with the local production of offspring (Caley et al., 1996). Persistence of local populations depends on the fecundity of lobsters elsewhere. Additionally, growth is determined by the local dynamics and conditions.

For a detailed description of the species see Section 1.2 in Chapter 1.

4.2.2 Data

4.2.2.1 Empirical data measured during this study

Length-frequency data were collected between November 2009 and December 2011 from 2116 individuals of *P. gracilis* at the northern coast of mainland Ecuador, in Cape San Francisco, at the Galera-San Francisco Marine Reserve (Figure 4.3). The first year data proceed from fisheries landings collected with the compliance and help of the local artisanal fishermen. In the second year, a conservation agreement was established, which enabled the fishermen to create a non-take zone and monitor periodically the lobster population. Lobsters were caught by traditional fishing, using one gillnet of 10.16 cm mesh size (stretched length), of 1.5 m width and 170 m length. The net was extended over mixed muddy-rock floor substrata at a depth between 3 and 10 m and left overnight for 10 to 12 hours. Captured lobsters were generally alive, these were measured and then released back to the sea. For each individual captured, the carapace length (CL) and total body length (TL) were recorded (for lobster body parts see Figure 4.2C). I refer to the data as "Luna, this study" and it is summarized in Table 4.1.

Additionally, I used a set of mark-recapture data from the Galapagos Marine Reserve. This program was run by the Charles Darwin Foundation and the Galapagos National Park Authority between 2001 and 2007. 57 females and 56 males of *P. gracilis* were caught by means of SCUBA diving and individuals were marked with a numbered T-floy tag and released. The number of *P. gracilis* recaptured was too low to make a reliable estimation of growth and therefore the resulting publication by Hearn & Murillo (2008) did not include the green spiny lobster. In this study, I refer to the data as "Hearn, not published" and it is summarized in Table 4.1.

4.2.2.2 Literature survey to complete the data set

I searched for all available publications about the green spiny lobster P. gracilis in Ecuador. I included institutional reports from the National Fisheries Institute (INP in Spanish), the Galapagos National Park Authority and the Charles Darwin Foundation. Likewise, peer reviewed international journals, publications in local scientific journals, as well as thesis manuscripts and NGO reports were considered. The earliest study dates from 1966 and the latest from 2015 and range from different places along the mainland coast and the Galapagos Marine Reserve. While all of them were used for consultation, only five studies (three from mainland Ecuador and two from Galapagos) met the selection criteria.

I selected those studies that presented length-length linear relation equations for the green spiny lobster, the methodology for measuring the different body parts, the number of individuals assessed and their size ranges. All studies are considered for the year when data were taken. Each study from mainland Ecuador represents a locality where data were taken, except for Loesch & Lopez (1966) which presents the analyses altogether for eight important fishing ports (Figure 4.3). The studies from Galapagos also present all data together without differentiating each monitored location, and only mentioning that most of the data come from the west-central archipelago where the green spiny lobster is more abundant. References to the selected studies, the names of the sampled localities, the date when data were taken, the number of lobsters measured by sex, their size ranges and the original

equations are presented in Table 4.1 in columns one to six. Locality of surveyed sites in the published studies is presented in Figure 4.3.

4.2.3 Data transformation

The selected studies defined the body parts of the lobster differently. Total length were measured in two different ways (Cruz, 2002; Holthuis, 1991), whereas all studies defined and measured the tail and carapace length in the same way (Figure 4.2). However, most of the studies in Ecuador only measured the total and tail length as needed for complying with the national minimum landing size regulation (Ministerio de Comercio Exterior Industrialización y Pesca, 2001). Figure 4.2 shows the lobster body parts as defined by FAO (Figure 4.2A, B) and the Ecuadorian authority (Figure 4.2C) according to the definitions of the selected studies. I calculated a conversion factor to compare different studies of morphological relationships of the green spiny lobster in Ecuador.

The main difference in the measurements is the inclusion or not of the antennular plate in the carapace and total length (see Figure 4.2A-C). It was possible to access a section of the Galapagos data base (Hearn, not published) where carapace measures of the same individual were taken with and without the antennular plate, to calculate a conversion factor of the form:

$$CL_{ap} = 1.3\ CL$$

or for the conversion of the total length:

$$TL_{ap} = 1.11\ TL$$

Where CL_{ap} is the carapace length and TL_{ap} the total length, both including the antennular plate as in Figure 4.2B and 4.2C. CL and TL don't include the antennular plate (Figure 4.2A). The factor is equally applicable for both sexes. I chose to convert all equations in the total length including the antennular plate TL_{ap} as a function of the tail length, since that is the way established by the Ecuadorian Ministerio de Comercio Exterior Industrialización y Pesca (2001) in the Lobster Agreement No. 182. The resulting comparable linear regression equations show the relation between the tail length and the total length from each study site and my own are presented in Table 4.1, column 7. These equations are standardized and enable a comparison between studies of body lengths' parts.

Table 4.1. Selected studies to compare morphological relationships equations. The table shows the original equation presented in each study and the standardized equations using the conversion factors presented in this study, where CL_{ap} is the carapace length and TL_{ap} the total length, both including the antennular plate see Figure 4.2B and 2C. CL and TL don't include the antennular plate (Figure 4.2A).

Selected studies reference	Locality	Date of data	n		Size range (mm)		Original length-length equations presented in studies	Standardized length-length equations calculated for this study
			females	males	females	males		
Loesch & Lopez, 1966	Data mixed from several localities in Mainland Ecuador	Mar. 1962-Mar. 1963	64	96	220-370TL_{ap}	220-370TL_{ap}	$TL_{ap\_female}(cm) = 3.42 + 2.214CL_{ap\_female}(cm)$ $TL_{ap\_male}(cm) = 7.26 + 1.746CL_{ap\_male}(cm)$ $TL_{ap\_female}(cm) = 2.51 + 1.559Tail_{female}(cm)$ $TL_{ap\_male}(cm) = -1.74 + 1.912Tail_{male}(cm)$	$Tail_{female}(mm) = -16.18 + 0.6417TL_{ap\_female}(mm)$ $Tail_{male}(mm) = 9.0658 + 0.5231TL_{ap\_male}(mm)$
Figueroa & Mero, 2012	El Mangle-Puerto Cayo and Puerto Lopez Salango	Jun.-Sep. 2010	415	288	42-121CL	42-121CL	$Tail_{female}(mm) = -7.734 + 1.7132TL_{female}(mm)$ $Tail_{male}(mm) = 7.2394 + 1.3936TL_{male}(mm)$	$Tail_{female}(mm) = -3.2921 + 0.5682TL_{ap\_female}(mm)$ $Tail_{male}(mm) = 3.5000 + 0.5174TL_{ap\_male}(mm)$
Murillo et al., 2013	Anconcito	Sep. -Dec. 2012	337	370	70-340 TL_{ap}	110-320TL_{ap}	$CL_{female}(mm) = 0.4043 + 0.3302TL_{ap\_female}(cm)$ $CL_{male}(mm) = 0.9534 + 0.3948TL_{ap\_male}(cm)$	$Tail_{female}(mm) = -5.2156 + 0.5705TL_{ap\_female}(mm)$ $Tail_{male}(mm) = 12.31 + 0.4871TL_{ap\_male}(mm)$
Luna, this study	Cape San Francisco	2009-2012	643	1311	103-257TL_{ap}	77-294TL_{ap}		$Tail_{female}(mm) = -1.0618 + 0.5804TL_{ap\_female}(mm)$ $Tail_{male}(mm) = 2.2042 + 0.5365TL_{ap\_male}(mm)$
Bautil, 2003	Data mixed from several localities in Galapagos	2002	144	151	120-270 $Tail$	120-280$Tail$	$TL_{ap\_female}(cm) = -0.9331 + 1.7193Tail_{female}(cm)$ $TL_{ap\_male}(cm) = -0.1623 + 1.7596Tail_{male}(cm)$	$Tail_{female}(mm) = 5.4196 + 0.5817TL_{ap\_female}(mm)$ $Tail_{male}(mm) = 0.9422 + 0.5683TL_{ap\_male}(mm)$
Parque Nacional Galapagos, 2015	Data mixed from several localities in Galapagos	1995-2012	1023	1022	40-472TL_{ap}	40-491TL_{ap}	$TL_{ap\_und.sex}(cm) = 1.9418 + 2.0468Tail_{und.sex}(cm)$	
Hearn, not published	Data mixed from several localities in Galapagos	2001-2007	57	56	157-400TL_{ap}	188-410TL_{ap}		$Tail_{female}(mm) = -20.79 + 0.6398TL_{ap\_female}(mm)$ $Tail_{male}(mm) = 30.95 + 0.4317TL_{ap\_male}(mm)$

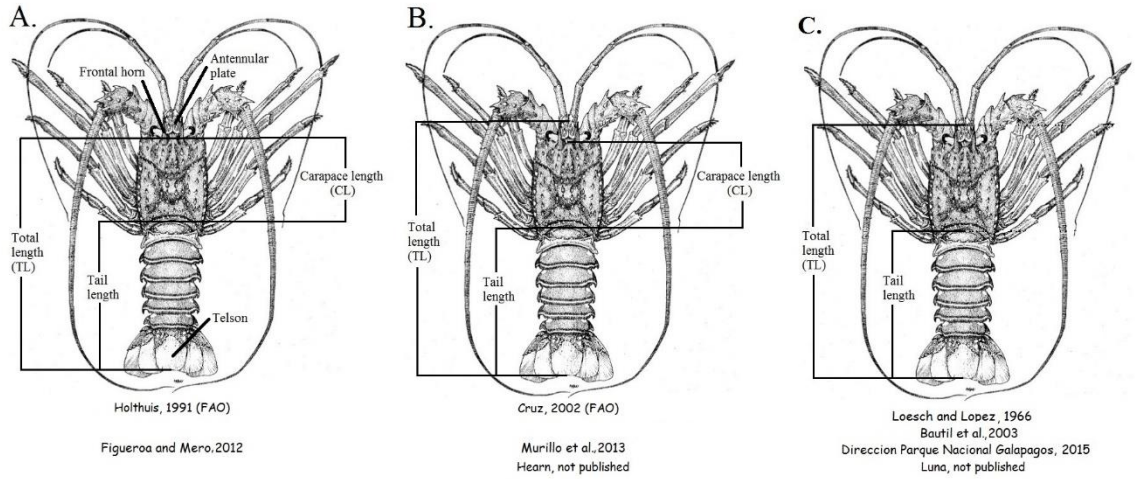

Figure 4.2. Different definitions of the extent of the lobster body parts used in the selected published studies and our own study. Note that tail length is equal whereas the carapace and total length vary by including or not the antennular plate. A. is the official definition from FAO defined by Figueroa and Mero (2012). B. is used by Murillo *et al.* (2013), and C. by Loesch and Lopez (1966), our study and the Galapagos studies. The Ecuadorian Environmental Ministry Agreement No.182 where lobster fisheries regulations are established, defines the minimum landing total body length as in C. The green spiny lobster illustration is from Holthuis (1991).

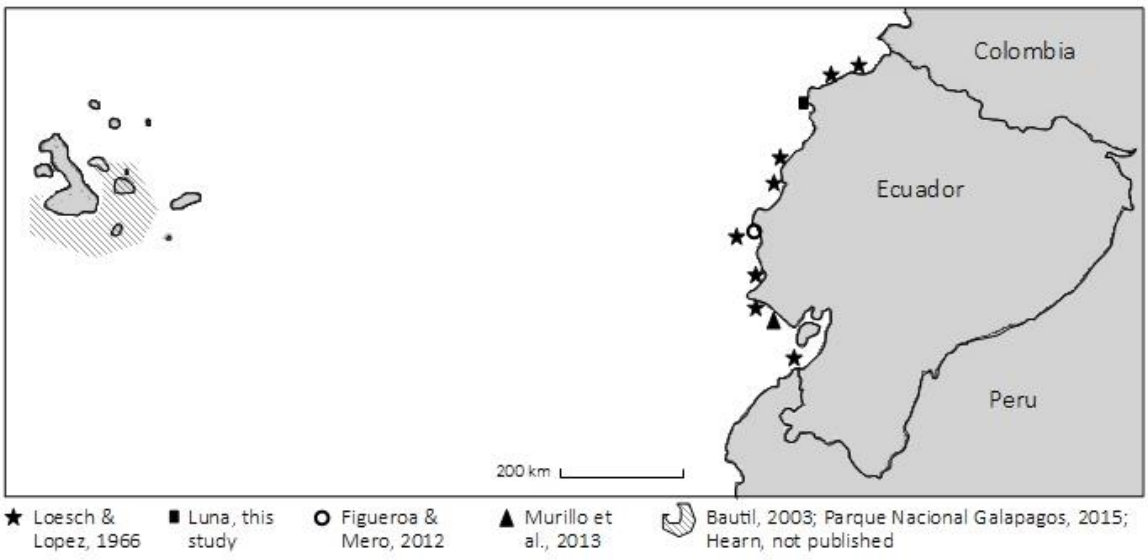

Fig. 4.3. Locality of the sites presented in the publications considered in this study:"black diamonds" represent sites monitored by Loesch and Lopez (1966), "red triangle" show the locality at Manabi in Figueroa and Mero (2012), "red oval" points Anconcito in Murillo et al. (2013), "red star" represents our own study site RMGSF in Luna, this study, "red rectangle" show the locality of all Galapagos studies.

4.2.5 Data analysis

In order to examine the variations of length-length relations among sexes and sites, I performed first a linear regression analysis between tail length (dependent variable) and total length (explanatory variable) for females and males separately. A comparison of the tail length / total length ratio between all available data sets were used to analyse changes in capture size over time. This analysis was completed by a multiple comparison of the slopes of another suite of linear regression models explaining the tail length with total length and locality as categorical variable. This multiple comparison of the slopes informed about the statistical significance of differences between the length-length ratios of all available studies.

A multiple regression model was performed in order to analyze the effect of locality, sex, age and mean sea surface temperature (SST) on the tail length/total length. Mean SST values specific for each site and for the period of time when data were taken, were extracted from the AquaModis satellite online data base using the free software SeaDAS (Baith et al., 2001). Two methods were used to analyse significance of factors since their validity for model selection is discussed:

1) Models were stepwise backward reduced to identify the most important factors. The strength of each particular explanatory factor was finally examined by ranking all sums of squares of the ANOVA model and the Akaike information criterion (AIC).
2) Models were compared by means of R^2 and an ANOVA.

In order to check the suitability of the models, the residuals were previously checked against normal distribution and heteroscedasticity. As a result of these tests, I normalized the data distribution by taking the natural logarithm of all tail length / total length values for the multiple regressions. Collinearity of the factors was tested using the variance inflation factor (VIF). If VIF returns a value larger than 10, multicolinearity is strongly suggested. Since mean SST is correlated to localities, but not to age and sex, the effects of mean SST and locality on the tail length/total length in separate models were tested. Table 4.2 describes the variables used in the two models. All statistical analyses were performed using R 3.0.2 (http://www.R-project.org/).

$\boldsymbol{Model\ 1}$: $\frac{Tail}{total}$ $length\ ratio\ is\ modeled\ as\ locality * sex * age$

$\boldsymbol{Model\ 2}$: $Tail/total\ length\ ratio\ is\ modeled\ as\ mean\ SST\ at\ each\ locality * sex * age$

Table 4.2. Description of the variables considered in the models.

	Variable name	Variable type	Levels	Observations
Dependent	tail length/total length	continuous	1396 measurements	The natural logarithm was taken for normalizing the distribution.
Independent	Locality	categorical	Six: 1. Data mixed from several localities in Mainland Ecuador (Loesch & Lopez, 1966), 2. El Mangle-Puerto Cayo and Puerto Lopez Salango (Figeroa & Mero, 2012) 3. Anconcito (Murillo et al. 2013) 4. San Francisco (Luna, this study) 5. Data mixed from several localities in Galapagos (Bautil, 2003) 6. Data mixed from several localities in Galapagos (Hearn, not published)	Includes various unknown (not measured) location-specific variables. The only variable measured is sea surface temperature (SST).
Independent	sex	categorical	Two: female and male	
Independent	age	continuous	Age is represented as length, data show 151 size clases	Expressed by the carapace length of the lobsters measured at each site. Logarithm for normalizing the distribution.
Independent	Mean SST	continuous	Four	Mean temperature values correspond to localities. In the studies where data from several localities were mixed, also a mean SST from all monitored localities was calculated.

4.3 RESULTS

Minimum landing size (MLS) is established by each country to assure that individuals reproduce before being exploited. In Ecuador, MLS is based on a total length of 260 mm and a tail length of 15 mm. Simulated linear regressions suggest that males in all selected studies reached a legal tail length of 150 mm at a larger total size than the legally established of 260 mm (Figure 4.4A). In females, this effect is weaker (Figure 4.4B). The results suggest that at the north, a lobster of 260 mm of total length has a tail size of 150 mm. Whereas towards the south, larger lobsters have to be fished in order to convey to the MLS of 150 mm minimum tail length management rule (Table 4.3).

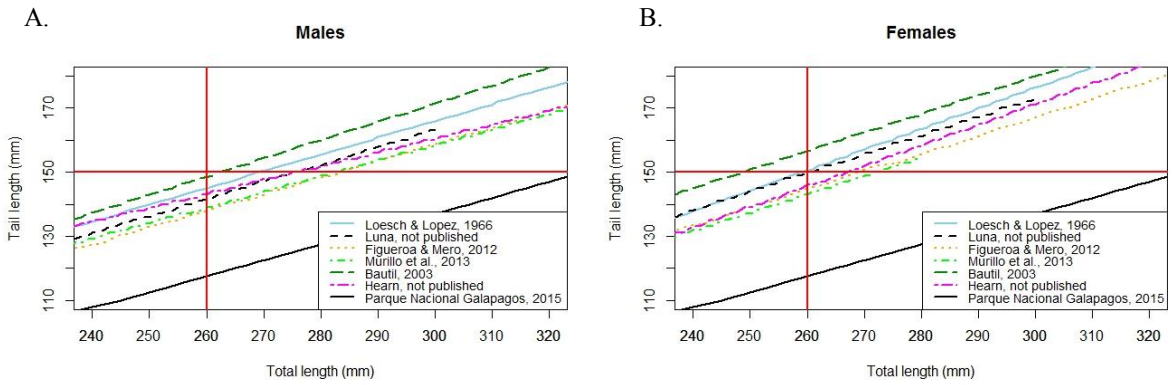

Figure 4.4. Linear regressions for each sex and for every monitored locality presented in the selected studies: A. Males and B. Females. The regression that represents the Galapagos DPNG study is the same for females and males and shows a large difference from the others suggesting some error. Red lines mark the minimum landing sizes as 260mm total length and 150mm tail length.

Table 4.3. The total length that female and male lobsters should have in the different localities along mainland Ecuador and Galapagos in order to fish a legal tail length of 150mm. In most cases individuals have to be larger than the total length legal size of 260mm.

Study	Site	Female TL (mm)	Male TL (mm)
Loesch & Lopez, 1966	Data mixed from several localities in Mainland Ecuador	260	270
Luna, this study	Cape San Francisco	260	275
Figueroa & Mero, 2012	El Mangle-Puerto Cayo and Puerto Lopez-Salango	269	284
Murillo et al., 2013	Anconcito	272	282
Bautil, 2003	Data mixed from several localities in Galapagos	248	262
Hearn, not published	Data mixed from several localities in Galapagos	267	276

The comparison of the tail and total length ratios suggest that they are significantly different among localities and that they have changed in time in both, the mainland coast of Ecuador and the Galapagos Islands (Figure 4.5). In the mainland, the oldest study with data from 1963 (Loesch & Lopez, 1966) has females with the largest $ln(tail/total\ length)$ ratio meaning that at that time females had longer tails in average with respect to their total body size. In the same way, the studies performed between 2009 and 2012 in the mainland coast suggest that females in Cape San Francisco, the

northern locality, have a larger tail in relation to their total body size than the females in the central (El Mangle-Puerto Cayo and Puerto Lopez-Salango) and the southern locality (Anconcito). Whereas, among males the variation in time and site seems to be weak (Figure 4.5). In Galapagos, the equations calculated by Bautil et al. (2003) suggest that between 1998 and 2001, when data were taken, individuals of both sexes had larger tails than the lobsters measured between 2001 and 2007 by Hearn, not published (Figure 4.5). The equation presented by the Galapagos National Park Office (DPNG 2015) shows a much different ratio than the other since it pools data from both sexes and several years. The comparison of the standardized linear regression slopes through multiple regression, that tested the tail length as a function of total length, showed statistically significant differences among all localities, time and between females and males (Table 4.4).

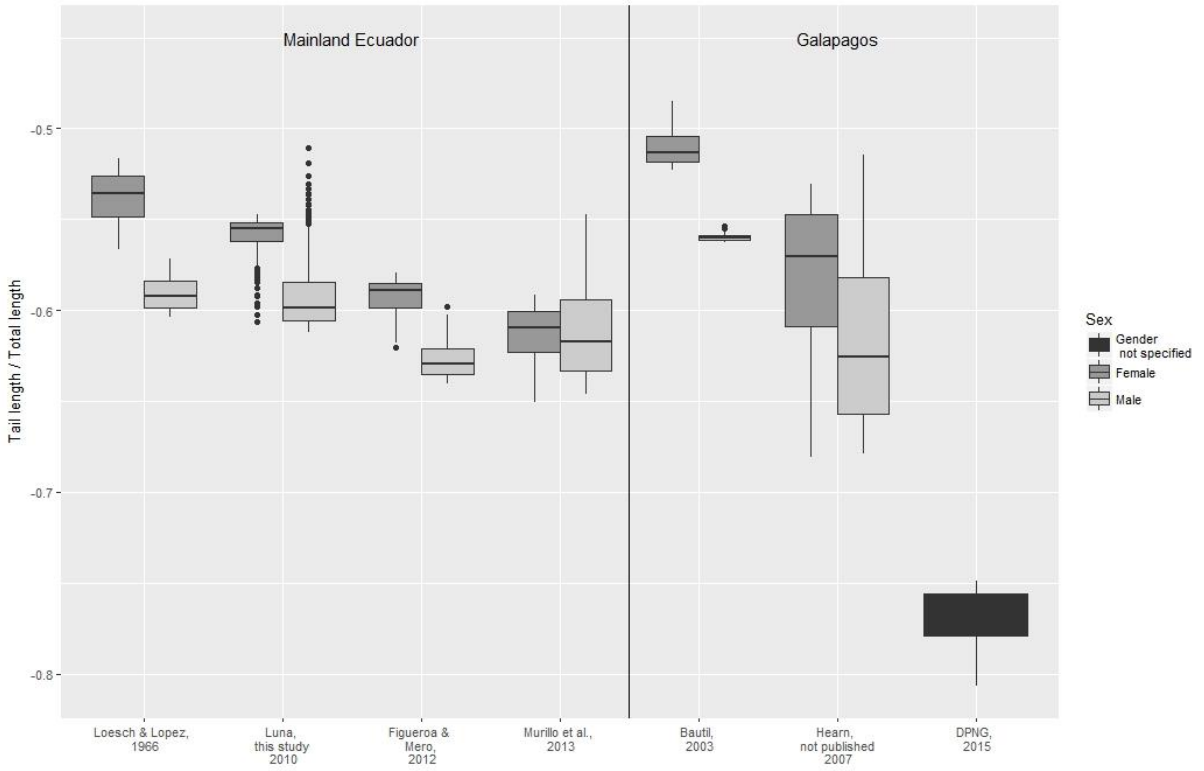

Figure 4.5. Tail-total length ratio in natural logarithmic scale for females and males of the green spiny lobster. Each pair of boxplots corresponds to every study selected. The equation presented in 2015 (DPNG-Direccion Parque Nacional Galapagos) for both sexes together, calculated from data taken between 1995 to 2012 shows a large variation suggesting some error and therefore is not comparable to the other studies.

Table 4.4. Linear model results to identify significant differences among the regression slopes of the published studies and our own. Results are presented for each sex since sexual dimorphism is significant. Linear regressions models described tail length as a function of total length and locality. For this comparison, I did not consider the Galapagos DPNG study since the equation that they presented was for both sexes together and it was expected to find an obvious, but misleading difference.

Females / Males	Loesch & Lopez, 1966	Luna, this study	Figueroa & Mero, 2012	Murillo, 2013	Bautil, 2003	Hearn, not published
Loesch & Lopez, 1966		$\beta = 6.133e-02$ $SE(\beta) = 7.819e-04$ $p-value = < 2e-16$	$\beta = -7.349e-02$ $SE(\beta) = 8.654e-04$ $p-value = < 2e-16$	$\beta = -7.121e-02$ $SE(\beta) = 8.580e-04$ $p-value = < 2e-16$	$\beta = -6.006e-02$ $SE(\beta) = 7.823e-04$ $p-value = < 2e-16$	$\beta = -1.994e-03$ $SE(\beta) = 7.888e-04$ $p-value = 0.0116$
Luna, this study	$\beta = -0.0133136$ $SE(\beta) = 0.0006427$ $p-value = < 2e-16$		$\beta = -1.216e-02$ $SE(\beta) = 4.850e-04$ $p-value = < 2e-16$	$\beta = -9.879e-03$ $SE(\beta) = 4.718e-04$ $p-value = < 2e-16$	$\beta = 1.269e-03$ $SE(\beta) = 3.137e-04$ $p-value = 5.61e-05$	$\beta = 5.934e-02$ $SE(\beta) = 3.296e-04$ $p-value = < 2e-16$
Figueroa & Mero, 2012	$\beta = -0.0057546$ $SE(\beta) = 0.0007706$ $p-value = 1.76e-13$	$\beta = -0.0190682$ $SE(\beta) = 0.0005256$ $p-value = < 2e-16$		$\beta = -2.282e-03$ $SE(\beta) = 6.001e-04$ $p-value = 0.000152$	$\beta = 1.343e-02$ $SE(\beta) = 4.857e-04$ $p-value = < 2e-16$	$\beta = 7.150e-02$ $SE(\beta) = 4.962e-04$ $p-value = < 2e-16$
Murillo, 2013	$\beta = -0.0360250$ $SE(\beta) = 0.0006980$ $p-value = < 2e-16$	$\beta = -0.0493386$ $SE(\beta) = 0.0004118$ $p-value = < 2e-16$	$\beta = 3.027e-02$ $SE(\beta) = 5.919e-04$ $p-value = < 2e-16$		$\beta = 1.115e-02$ $SE(\beta) = 4.725e-04$ $p-value = < 2e-16$	$\beta = 6.922e-02$ $SE(\beta) = 4.832e-04$ $p-value = < 2e-16$
Bautil, 2003	$\beta = 0.0451137$ $SE(\beta) = 0.0006415$ $p-value = < 2e-16$	$\beta = 0.0318001$ $SE(\beta) = 0.0003066$ $p-value = < 2e-16$	$\beta = 5.08683e-02$ $SE(\beta) = 5.242e-04$ $p-value = < 2e-16$	$\beta = 8.114e-02$ $SE(\beta) = 4.099e-04$ $p-value = < 2e-16$		$\beta = 5.807e-02$ $SE(\beta) = 3.307e-04$ $p-value = < 2e-16$
Hearn, not published	$\beta = -0.0914571$ $SE(\beta) = 0.0006647$ $p-value = < 2e-16$	$\beta = -0.1047706$ $SE(\beta) = 0.0003526$ $p-value = < 2e-16$	$\beta = -8.57024\,e-02$ $SE(\beta) = 5.523e-04$ $p-value = < 2e-16$	$\beta = -5.543\,e-02$ $SE(\beta) = 4.454e-04$ $p-value = < 2e-16$	$\beta = -13.65707e-02$ $SE(\beta) = 3.504\,e-04$ $p-value = < 2e-16$	

Multiple regressions showed a significant influence of all predictor variables and all their interactions. The stepwise model selection method didn't drop any of the parameters of the tested models. Detailed results for each model are presented in Table A4.1 in the Annex. However, the highest R^2 (0.9882) was given by the model using locality as a factorial variable. As such it is assumed that the variable "locality" comprises various site-specific environmental characteristics, among them mean SST. The models that tested mean SST, which I hypothesized can be used as the main site-specific variable responsible for explaining variations in tail length/total length, returned much lower fits (Table 4.5) and ANOVA showed that both models are significantly different from each other ($F = 6497.3, p-value < 2.2e-16$). Indeed, multiple regressions revealed that locality made the strongest contribution (> 40%) to explain variation on tail length/total length (Table 4.5). In contrast, when locality was replaced with mean SST, over 60% of the total variability remained unexplained (Table 4.5).

Table 4.5. Comparison of multiple regression models and the relative impact of each variable on the tail / total length variation, expressed in percentage. Locality is treated as a factor with six categorical levels, sex is a factor with two categorical levels and age is represented as the natural logarithm of the carapace length. The Galapagos equation where gender was not defined was excluded from the analysis.

	Model 1 Tail/total length ratio is modeled as locality * sex * age	***Model 2*** Tail/total length ratio is modeled as mean SST * sex * age
AIC	-22166.25	-14100.81
Multiple R-squared	0.9882	0.3829
Adjusted R-squared	0.9881	0.3808
p-value	< 2.2e-16	< 2.2e-16
Percentage of the variance explained by predictor variables		
Locality	44.47706	-
Mean SST	-	3.716763
Age	0.5886543	1.993131
Sex	15.68548	15.87623
Age : sex	11.11132	11.85705
Age : locality	0.2384475	-
Age : mean SST	-	0.07553837
Sex : locality	7.308142	-
Sex : mean SST	-	0.526843
Age : sex : locality	19.41417	-
Age : sex : mean SST	-	4.248819
Residuals	1.176737	61.70562

4.4 DISCUSSION

Our results are based on the analysis of the five published studies along the coast of mainland Ecuador and Galapagos (Bautil et al., 2003; DPNG, 2015; Figueroa & Mero, 2013a; Loesch & Lopez, 1966; Murillo Posada et al., 2013) and two additional data sets, one conducted by Luna and the other one by Hearn. Length-length linear relations equations were examined to investigate patterns of the green lobster morphological variations in time and space and its possible implication on the minimum landing size regulation. The main findings of this study are that the ratio between the tail size and the total length of the green spiny lobsters is significantly different in time and among localities, decreasing with temperature from north to south at the mainland coast of Ecuador. It was however, not possible to identify sea surface temperature as the main factor causing these variations as hypothesized in the beginning. Therefore a combination of site-specific characteristics are needed to explain differences in space and time. These findings are important for managers if they want to revise and implement a more appropriated minimum landing size (MLS).

The authors of the selected studies formulated morphological relationships using different lobster body parts which additionally, were measured differently. As with any analysis, data and methodologies have to be carefully examined to be able to compare them to each other. I estimated a conversion factor in order to standardize equations. This limitation proved to be an opportunity for spotting and addressing problems in the management and fisheries reporting regime. Harvest estimations are generally reported as the total catch in a fisheries season. In the case of lobsters, total catch is the total weight caught considering only the tails or the whole individual. Morphological relation equations are used to estimate sizes and weights from monitoring data. The certainty of harvest reports and projections may decrease if the used morphological equations are miscalculated, presented for females and males together, or are used for several local populations which are different among each other.

Morphometric variations among spiny lobster local populations within regions have been also shown by Matthews et al. (2003), Garcia-Rodriguez and Perez-Enriquez (2004 and 2008), Pollock (1993) and Barkai and Branch (1988). The magnitude of these variations becomes important and needs to be monitored when it turns significant for adapting minimum landing sizes. Estimations of the tail and total lengths using the corresponding morphological relationship equations for the different studies in Ecuador, returned results that don't entirely support current minimum landing size regulations. Lobsters caught at the south of Ecuador would have to be ca. 20 mm larger than the ones in the north in order to convey to the management rule of 150 mm of tail length. This findings are relevant to any revision of MLS regulation since worldwide changes of the MLS for carapace, tail, or total length are rarely larger than one centimeter. In Ecuador for example, MLS was changed only once, from 250 mm to 260 mm total landing size in 1982.

The pattern of larger tails in the north of Ecuador and decreasing towards the south, follows the pattern of SST. At the northern coast, sea surface temperatures are higher and vary in only 1°C among seasons. Whereas at the south, where the cold Peruvian current has more influence, temperatures are ca. 4 degrees lower and vary also in 4°C among seasons. The trend that spiny lobster growth rates are positively associated with temperature has been proved before (Green et al., 2014; Briones-Fourzán & Lozano-Álvarez, 2003; Pollock, 1986; Lellis & Russell, 1990; Hartnoll, 1982, 2001; Mayfield, Branch, & Cockcroft, 2000). However, my hypothesis that water temperature can be used as the most important variable to explain variations in the tail-total length relation was rejected as shown in the results of the multiple regression models. The alternative explanation is that there are other site specific factors or

their combined effect that influence fluctuations of the lobster body length ratios. The model which includes all types of site specific characteristic in a factorial variable, explains better the tail-total length variations found. However, it was not possible to detect the site-specific factors or combination of factors which play a key role in explaining and predicting morphological relation variations.

In nature, site-specific influences merge and their synergistic effects on the environment and the lobster population dynamics might be more difficult to predict (Pollock 1986). For example, temperature can as well contribute to the variation in food availability and benthos biomass has been shown to be positively correlated to lobster growth increments (Newman & Pollock, 1974; Pollock, 1986). Furthermore, Barkai & Branch (1988) and Beyers & Goosen (1987) found that it is not only the benthos biomass which enhances growth, but most importantly the benthos type which is edible by the lobster and which provides the highest caloric input, overall at high lobster densities. Chittleborough (1976) and Pollock (1986) found that after a certain density limit, individual growth weakens, suggesting a density-dependent growth. In Guerrero-Mexico, Briones-Fourzán & Lozano-Álvarez (2003) have shown that annual productivity increase in one site, provokes high immigration. Subsequent higher density causes scarcity of food and lower growth increments. As a result, growth increments in the green spiny lobster *P. gracilis* varied significantly among two sites separated only by 2.5 km from each other. In consequence, I recommend that future investigations gather quantitative information about other relevant variables, among them site-specific benthic type and biomass, lobster densities and predator diversity and abundance. These medium and long-term data can contribute to simplify and narrow models for simulating morphological variations and their potential effects on populations' dynamics and thus on fisheries performance.

To further investigate the effect of environmental variables on relative growth patterns of lobster and their impact on management measures, like the minimum landing size regulations, I recommend the standardization of measurement and reporting procedures in national and regional scales (regional defined as the geographical distribution of each lobster species). Furthermore, measurement methods should be thoroughly described in publications and reports. This is important when comparing populations in order to assess and plan management of an organism which population dynamics go beyond political limits. Moreover, if fishermen and control authorities are to comply with a regulation based on size, it has to be clearly and consistently determined. Analyses and reports of morphological relations by sex, time, and site separately allow to capture variations which may contribute to a better understanding of the dynamics and behavior of the species. In addition, it can also help to reveal differentiation of populations or stocks. At the same time, I recommend to explore and adjust length-length relations regularly, since results suggest that they change in time as well as in geographical space. This is important for applying appropriate management measures, for assessing their effectiveness with as less uncertainty as possible, and for adapting them accordingly.

To decrease uncertainty in measurements and harvest calculations, I propose to consider measuring the carapace length in addition to the tail and total length. In the Caribbean, Mexico, Panama, the carapace, and not the tail length, is used as enforcement rule, since the latter is flexible and subject to measurement errors (Cruz, 2002; Guzmán et al., 2008). Additionally, there are differences among sexes in tail length. As females attain sexual maturity they develop larger and heavier tails to be able to carry eggs. Adding a minimum landing size regulation based on the carapace length may be a step towards standardization of measurements and regulations in the region where *P. gracilis* is distributed. In that way, population analysis and harvests reports may be comparable and management planning and enforcement may gain strength.

In conclusion, I recommend to 1) standardize lobster size measurement procedures; 2) revise regulations' texts to write them accordingly; 3) analyse and report morphological relations for sex,

time, and site separately; 4) explore and adjust morphological relations regularly; 5) use carapace length as a more stable MLS measure, nevertheless have in mind that the relation to other body sizes might change in time and space and therefore regular monitoring of all body parts is pertinent.

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Annex

Table 4.1. Multiple linear regression models testing locality as possible cause for the variation of the tail-total length ratio. Location is treated as a factor with six categorical levels, sex is a factor with two categorical levels, and age is represented as the natural logarithm of the carapace length. The Galapagos equation were gender was not defined, was excluded from the analysis.

Model 1: tail /total length ~ locality * sex * age						
Predictor variables			β	SE (β)	t-value	p-value
Intercept			-1.057685	0.018116	-58.383	< 2e-16
Age			0.115347	0.004018	28.710	< 2e-16
Sex			0.708663	0.022232	31.876	< 2e-16
Locality	Figueroa & Mero, 2012	El Mangle-Puerto Cayo and Puerto Lopez Salango	0.330215	0.019470	16.960	< 2e-16
	Murillo et al., 2013	Anconcito	0.202132	0.018990	10.644	< 2e-16
	Luna, this study	Cape San Francisco	0.432780	0.018233	23.736	< 2e-16
	Bautil, 2003	Data mixed from several locations in Galapagos	0.686831	0.018719	36.692	< 2e-16
	Hearn, not published	Data mixed from several localities in Galapagos	-0.343523	0.019047	-18.036	< 2e-16
Age : sex			-0.167575	0.004886	-34.297	< 2e-16
Age : locality	Figueroa & Mero, 2012	El Mangle-Puerto Cayo and Puerto Lopez Salango	-0.084380	0.004337	-19.456	< 2e-16
	Murillo et al., 2013	Anconcito	-0.057518	0.004240	-13.566	< 2e-16
	Luna, this study	Cape San Francisco	-0.098312	0.004052	-24.264	< 2e-16
	Bautil, 2003	Data mixed from several localities in Galapagos	-0.146081	0.004149	-35.208	< 2e-16
	Hearn, not published	Data mixed from several localities in Galapagos	0.066453	0.004223	15.734	< 2e-16
Sex : locality	Figueroa & Mero, 2012	El Mangle-Puerto Cayo and Puerto Lopez Salango	-0.469988	0.024414	-19.251	< 2e-16
	Murillo et al., 2013	Anconcito	-0.057636	0.023506	-2.452	0.01429
	Luna, this study	Cape San Francisco	-0.543987	0.022413	-24.271	< 2e-16
	Bautil, 2003	Data mixed from several localities in Galapagos	-0.871636	0.023307	-37.398	< 2e-16
	Hearn, not published	Data mixed from several localities in Galapagos	0.834289	0.023520	35.472	< 2e-16
Age : sex : locality	Figueroa & Mero, 2012	El Mangle-Puerto Cayo and Puerto Lopez Salango	0.104875	0.005405	19.405	< 2e-16
	Murillo et al., 2013	Anconcito	0.016945	0.005201	3.258	0.00114
	Luna, this study	Cape San Francisco	0.117242	0.004939	23.740	< 2e-16
	Bautil, 2003	Data mixed from several localities in Galapagos	0.192738	0.005116	37.672	< 2e-16
	Hearn, not published	Data mixed from several localities in Galapagos	-0.177802	0.005167	-34.412	< 2e-16
Residual standard error: 0.004403 on 2021 degrees of freedom, Multiple R-squared: 0.9882, Adjusted R-squared: 0.9881 F-statistic: 7379 on 23 and 2021 DF, p-value: < 2.2e-16						

CHAPTER 5

5 CONCLUDING DISCUSSION

This is the first study with a regional perspective about the green spiny lobster *P. gracilis* combining science and fisheries practices for finding effective management measures. *P. gracilis* contributes to the commercially important artisanal fisheries in the Eastern Tropical Pacific -ETP (FAO, 2017). Despite there are regulations in place, most of the green spiny lobster fisheries in the ETP report alarming high percentages (between 60 and 98%) of lobsters under the minimum landing size (MLS) caught in the wild. It becomes particularly important to gain a regional overview, coordinate management, and regulation enforcement when considering that the persistence of spiny lobster populations at one locality does not only depend on the local management efforts. Green spiny lobster populations in the ETP are interconnected through a pelagic larval phase (*Phyllosoma*). During this phase that lasts for around nine months, *Phyllosoma* travel for hundreds to thousands kilometers. Thus, this allows for broad dispersal of the *Phyllosoma* and interconnection to other populations in the ETP.

In this study, I explore the effect of the current and potential management regulations, the patterns of regional and country level variations, and possible environmental and geographic causes for those variations. The aim is to evaluate the current measures and identify considerations to adapt regulations.

5.1 Major findings

The best suit of regulations to maintain the highest abundance, production of offspring and catch is to protect juveniles and egged females, and to establish a MLS that assures the reproduction of individuals before being extracted. This is true if the MLS is calculated and implemented at an age or a size larger than the SOM, for allowing individuals to reproduce one to three times before being extracted. An incorrect estimation of MLS, i.e. smaller than SOM or much larger than SOM, could lead the population to collapse or to under exploitation.

Fishing effort is the main factor influencing the population size and the production of offspring. It has been proven that it is as well not easy to control and manage (Sundelöf et al., 2015). At low levels of fishing effort, spiny lobster population presents the highest abundance and production of offspring. In a scenario where a correct MLS and a moratorium of egged females is in place, catch is maximized at a medium fishing effort. Higher fishing effort will not result in additional catch, but also not in lower catch. The absence of egged female protection maximizes the catch only at an intermediate level, a higher and lower efforts reduce the catch. Establishing an accurate MLS, in combination with egged female and juvenile protection, will secure the population and the catch even under high fishing effort.

MLS represent the size or weight at which it is optimal to extract an individual in terms of catch and to assure that the individual has contributed to the replenishment of the population. Therefore, the estimation of MLS is informed by the SOM and yield-per-recruit assessments. SOM estimates the size at which a proportion of 50% of the females in a population have attained sexual maturity. Yield-per-recruit assessments can return the size, age or weight at which a cohort produces the highest yield and biomass under varying levels of fishing mortality. Size, age, and weight of lobsters are used in morphological relationship models to calculate additional body parts of lobsters used for control and commerce.

Literature review at a regional scale in Chapter 3, showed that morphological relationships vary along the distribution of the green spiny lobster in the Eastern Tropical Pacific. The meta-regression in the meta-analysis revealed that the relationship of length to length and length to weight are more variable at northern latitudes, where the mean annual sea surface temperatures are higher than at lower temperatures at the Equator. Reported SOM data in the region didn't follow this same pattern as was hypothesized. It showed no relation to latitude, longitude, Chlorophyll a concentration, or sea surface temperature. However, SOM was reached at smaller sizes when the size at first maturity was also smaller. This is particularly important to keep in mind when using SOM to establish the MLS. Decreasing the MLS based on a smaller SOM may, in time, worsen the population state and press the population to smaller reproduction sizes. Larger females produce larger eggs which develop into larger larvae therefore, larger females may produce more viable offspring in comparison to the amount and quality of eggs produced by smaller females (Agnalt, 2008; Moland et al., 2010; Lyons et al., 1981). In this case, adapting the MLS to a smaller size would officially support shifting the baselines of lobster reproduction.

At a national scale, a closer exploration of the morphological relationships revealed that the ratio between the tail size and the total length of the green spiny lobsters is significantly different in time and among localities, decreasing with temperature from north to south at the mainland coast of Ecuador. It was however, not possible to identify sea surface temperature as the main factor causing these variations as hypothesized in the beginning. Therefore, a combination of site-specific characteristics are needed to explain differences in space and time. These findings are important for managers if they want to revise and implement a more appropriated minimum landing size (MLS).

5.2 Evaluation of the methodology

In Chapter 2, the B52 Spiny Lobster individual based population viability analysis was applied to assess the effect of fisheries practices and management scenarios on the population dynamics of the green spiny lobster *P. gracilis* in the ETP. The modelled scenarios were 1) "legal fishing", in which a MLS and an egged female moratorium are enforced, 2) "fishing egged", with no egged female moratorium, 3) "fishing juveniles", in which no MLS is enforced, but an egged female moratorium is in place, 4) "worst case", without a moratorium and MLS, and a 5) "no fishing" scenario. In Chapter 3, a meta-analysis was used to compare various scientific studies conducted in the ETP investigating spiny lobster morphological relations such as length-length and length-weight. With a meta-regression analysis, as part of the meta-analysis, I investigated the patterns and causes of heterogeneity among studies. Chapter 4 further investigates length-length relationships and potential factors causing variations at a country level scale by means of single and multivariate regressions. The following paragraphs give a general description and evaluation of the three methods used.

Individual based models are appropriate for conducting population viability analyses when it is important to capture individual variability in the life history parameters (Sundelöf et al., 2015; Berger

et al., 2008; DeAngelis & Grimm, 2014). In this case, reproduction, production of offspring, as well as mortality was age dependent and driven by probabilities. The B52 model was implemented in Vortex 10, a free software developed by the Chicago Zoological Society and supported by the IUCN. Several studies have evaluated the conservation status of endangered species, evaluated and ranked management scenarios and calculated the risk of extinction or explosion of populations. Vortex 10 offers a structure to be filled with data that describes the life history of the investigated species (see ODD in Chapter 2, Section 2.2.4 The B52 Spiny Lobster model, for a detailed description of the model). Depending on the amount and quality of information available, the population dynamics can be modelled at different levels of complexity. Comparisons of the model results to empirical data showed that my model represent in an acceptable way the spiny lobster population behavior, although comparisons were only possible for a worst case scenario, where no regulations are enforced. Other comparisons were not possible since no fisheries independent data were available in the region.

I modelled the population dynamics in the different fisheries scenarios with external input of offspring and without external influence. The first option is more realistic, however there is no information of the amount of offspring that enters every year each population, which populations are interconnected, and what is the relative importance of each population. The B52 model showed to be more sensitive to variations in mortality and percentage of females available to reproduce.

A limitation of applying Vortex 10 to this case study is that, since the model has a fixed interface, it is more difficult to make direct adaptations tailored to the research or species in question. For example, in this case it was necessary to transform all size data to age. This brought two further limitations. The first one was that it was not possible to retrieve the age structure of the harvested individuals per year in order to back calculate age to size and to weight in order to report the yield as the catch in weight. The second limitation is that considering that size increments in a year vary among individuals (Sheehy et al., 1999), localities (Briones-Fourzán & Lozano-Álvarez, 2003) and with age, it is possible to miss detail by this transformation. Furthermore, age at size relations in the ETP reported in the literature and in comparison to my calculations using empirical data, were different among each other. This turned to be important since it revealed that differences along the ETP, were not only present in the age at size relations but in morphological relations of length and weight at length. This led to the next research questions and the two next chapters in my study.

In Chapter 3, the independent studies presenting different morphological relations of length and weight at length were explored using a meta-analysis. The meta-analysis allowed to generalize results to a larger “population of studies” by combining the individual studies through the use of a normalized effect size. In this study, the effect size represented the correlation coefficient of the morphological relationships (r, transformed to the normalizing and variance-stabilizing Fisher’s z). Additionally, the meta-analysis allowed me to investigate publication bias and to identify and explain inconsistencies between studies. Finally, with this method I was also able to explore the source of the heterogeneity among studies, which is one of the main uses of meta-analysis in ecology.

A common criticism to meta-analysis is about their validity when combining heterogeneous studies (see for example Markow & Clarke, 1997; Koricheva et al., 2013). This limitation was overpowered by exploring the possible sources of heterogeneity. I learned that most of the variability across studies is due to genuine differences underlying the results rather than by chance (sampling error). The Q-test of heterogeneity, part of the meta-analysis, permitted to test if the structure of the data caused any effect on the results. The effect of year of sampling, combining two lobster species that share habitat in the ETP, as well as combining the different length-length and length-weight relations were not responsible for the observed heterogeneity. Through this method, it was possible to identify and eliminate the studies that showed publication bias. Finally, the meta-analysis allowed to test and

identify the environmental and geographic factors, also called moderator variables, responsible for the variation between studies. Furthermore, the meta-regression added to the analysis by showing the form of the relation at the regional level.

Chapter 4 adds to the exploration of the morphological variations in order to recognize potential pitfalls for management enforcement. Here, I concentrate on a case study at a country level scale in Ecuador. The single regression helps to reveal the relationships and compare these among studies to determine if their differences in time and space are significant. The multivariate analysis allows to test at a smaller scale if the effect of SST is consistent with the pattern revealed in Chapter 3.

A limitation in this chapter was that the morphological equations were not directly comparable. The various studies had defined and measured differently the spiny lobster body parts (see Chapter 4, Figure 4.2 for more detail). This was solved by calculating a conversion factor and transforming measurements and equations so that all adjusted morphological relationship equations refer to the same body parts(see Chapter 4, section 2.3 for more detail). The conversion factor estimation was based on a set of data from Galapagos (Hearn, not published) with the complete measurements of all lobster body parts. The transformed equations were used for all tests in this chapter.

5.3 Implications for spiny lobster fisheries management

Extraction of juveniles, in combination with extracting egged females, can lead to population collapse even with the input of offspring produced independently of the state of the adult population. These fishing practices should therefore be avoided. Larger mesh sizes or scape openings in traps for smaller individuals, as well as enforcing an egged female moratorium, should be a priority among management measures.

Fishing effort has the largest impact on the population abundance, the production of offspring and the catch. The protection of egged females slows the effect of an increasing effort. Additionally, a MLS that allows the reproduction of at least 50% of the females between one and three times per year, diminishes the impact of increasing fishing effort. The combined implementation of these regulations is especially important if there is no fishing effort regulation and control.

Key to the success of these regulations is the accurate estimation of MLS. To achieve this, it is necessary to standardize measurement methods (Figure 5.1 suggest a definition of lobster body parts), fisheries monitoring methods, and reports at a country-level and regional scale. Legislation in each country should be updated to include regional agreed standard definitions and methods, and regional agreements should be established in the frame of transnational management of the Eastern Tropical Pacific Marine Corridor (CMAR, Spanish acronym). Furthermore, I recommend that the estimation of MLS considers the regional variability revealed in this study. Populations at higher latitudes and higher temperatures show more variability in their body parts ratio. In practice, the consideration of this pattern can be included by using the precautionary approach and acknowledging in the regulation the range of variations. At the regional level, these results may aid to identify the appropriate management and to increase research regarding the interconnectivity among populations and their relative importance in order to identify more resistant areas where management should focus to assure the flux of larvae are maintained.

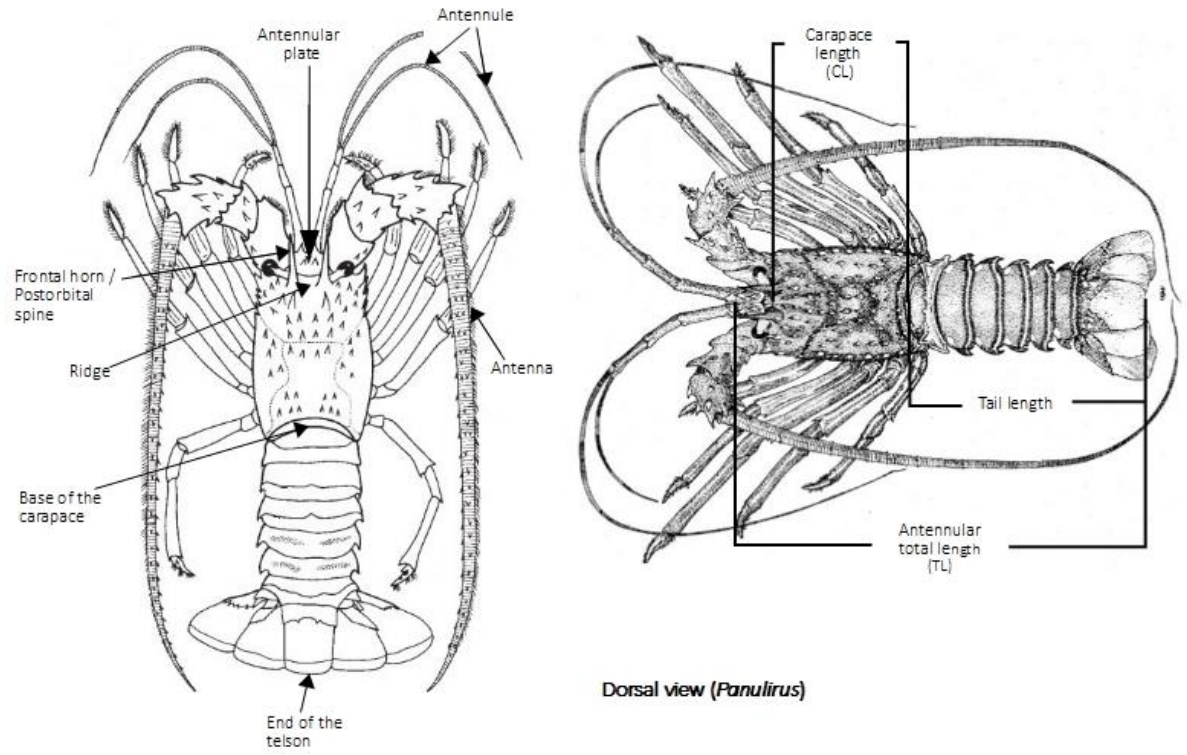

Figure 5.1. Lobster body parts based on Chan, 1998; Cruz, 2002; Holthuis, 1991. **Total length (TL)**, measured from the anterior part of the lobster from the base of the *antenulae* to the posterior margin of the *telson*. **Carapace length (CL)**, measured from the ridge between the frontal horns (also called postorbital spines) to the base of the carapace. **Tail length**, from the base of the carapace to the posterior margin of the *telson*. Note: Some body parts descriptions use the word *rostrum*. Panulirus sp. Don't have a *rostrum* (see Holthuis, 1991). I strongly encourage to "copy-paste" definition of the body parts and include the citation. I don't recommend to look for synonyms.

5.4 Outlook

The meta-analysis and the regression analyses showed patterns of variation of the morphological relations along a gradient of temperatures. The incorporation of these data in the individual based population viability analysis can inform relative growth, reproduction, production of offspring and variations in the catch, as well as contribute to explore the effect of rising temperatures in climate change. At the present, this is not possible to incorporate in the B52 model implemented in Vortex 10, since individuals are characterized by age and not by size. Therefore, an individual based population viability analysis model tailored for spiny lobsters could be developed.

As suggested by DeAngelis & Grimm (2014), modules for simulating the different life cycle events could be developed according to the availability and accessibility of spiny lobster population and fishery information. A modular design allows to link life-history events to incorporate levels of complexity. Moreover, such a model facilitates its tailoring for different species and therefore can become broadly used.

I learned that combining regional information can provide with useful insights to enlighten and facilitate management at a regional and country-level scales. The limitation here is that fishery reports are not standardized and not accessible. I recommend to opt for a politic of open data and make data bases accessible by all public, incorporating environmental, geographic, human use information, among other. This demands collaboration and standardization at local and regional levels.

Moreover, I proved that current management regulations are effective, however, populations are degrading along the region. Country-level reports suggest that one of their main challenges is to enforce and control regulations. Without doubt fisherman, local communities and groups as well as lobster consumers need to be involved in the management. Involvement can take several levels from just informing and raising awareness, to the participation in the problem definition, data collection and analysis.

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STATEMENT OF AUTHORSHIP

I hereby certify that I have authored this Dissertation entitled Population Dynamics and factors affecting spiny lobster small scale fisheries independently and without undue assistance from third parties. No other than the resources and references indicated in this thesis have been used. I have marked both literal and accordingly adopted quotations as such. During the preparation of this thesis I was only supported by the following persons:

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Additional persons were not involved in the spiritual preparation of the present thesis. I am aware that violations of this declaration may lead to subsequent withdrawal of the degree.

Dresden, 04.04.2018

Soledad Luna